COMPARATIVE ASPECTS OF ADJUNCTIVE BEHAVIOUR:

The Performance of Rats and Ferrets Under Response Non-Contingent Schedules of Food Delivery.

A THESIS PRESENTED TO

THE DEPARTMENT OF PSYCHOLOGY AND SOCIOLOGY

UNIVERSITY OF CANTERBURY

In partial fulfilment of the requirements for the Degree of

DOCTOR OF PHILOSOPHY

BY

LANCELOT IAN BRUCE MILLER

MAY 1978

ABSTRACT

In the contemporary study of animal behaviour there is an increasing awareness that laboratory-based and field-oriented approaches are compatible in both theory and method. The phenomenon of schedule-induced polydipsia belongs to a class of events termed "adjunctive behaviours." These behaviours have been considered causally, functionally and adaptively similar to the displacement activities that are familiar to Ethologists. In this thesis two aspects of schedule-induced polydipsia are examined from both a laboratory and a biological perspective.

Firstly, the temporal locus of schedule-induced polydipsia was investigated in rats and it was found to be concentrated predominently in the interval immediately following food ingestion. Methodological and theoretical aspects of this finding are discussed.

Secondly, the species-generality of schedule-induced polydipsia was tested using ferrets, but no evidence of the phenomenon was found in this species.

Rats and ferrets were then studied by the comparative method using observational techniques in a situation that produced polydipsia in the former, and the differences observed were discussed in relation to methodological and ecological factors.

Selective aspects of the various approaches to the study of animal behaviour are discussed in an appendix, as are some biological considerations of the two species used. It is concluded that laboratory and naturalistic approaches, when viewed in the evolutionary framework, provide a fruitful and balanced foundation for the study of animal behaviour.

ACKNOWLEDGEMENTS.

The assistance of many people have made this thesis possible. I wish to record my gratitude to Mr. Jim Pollard for his supervision of the research, and his helpful criticism during the initial writing. My thanks are also accorded to Dr. Rob Hughes and Mr. Neville Blampied for the advice and encouragement during the period of experimentation.

The contribution of the technical staff of the Psychology Department has been great, and my deepest thanks are due to them. In particular, the good services of Mr. Lawrie Foulds, Mr. John Barton, and the late David Watson deserve recognition. Further recognition of the diligent efforts of Mrs. Penny MacPherson and Mrs. Robyn Reid deserve a special credit for their care and interest in the welfare of the animal colony.

My gratitude is extended to the University Grants Committee for the provision of the Scholarship that financed the bulk of the research. To my present employers, the Justice Department, I wish to accord my appreciation for the generous provision of the time to finish writing the thesis. Special mention of the support and consideration of my colleagues and friends at the Regional Psychological Centre is necessary; and the understanding and encouragement of Mr. Harry Cohen deserves special recognition, not the least for his patient efforts to enable me achieve personal insight.

Finally, to my dearest Jeanette, I wish to record my debt, for your assistance in the typing and in the

analysis of the results, and for your patience and care over the months of writing. It is with my deepest love that I dedicate this thesis to you.

****

CONTENTS

Note to Reader
Pages are numbered chapter by chapter,
chapters are separated by pink pages,
appendices are separated by yellow pages.

CHAPTER

INTRODUCTION.

I A brief consideration of several contemporary issues that have challenged traditional psychological approaches to the study of animal behaviour, and a statement of the experimental strategy adopted in this thesis.

II SCHEDULE - INDUCED POLYDIPSIA.

A general introduction to the phenomenon of schedule-induced polydipsia and its relationship to displacement activities, a review of some important parameters and various explanatory accounts, and a discussion on the importance of investigating both the temporal locus and species - generality of this behaviour.

III GENERAL EXPERIMENTAL RATIONALE.

The general experimental procedure adopted to study the temporal locus and the species - generality of schedule-induced polydipsia, the problem of obtaining equivalent food deprivation levels in the two species studied and the design of a suitable paradigm and method of data analysis.

IV THE TEMPORAL LOCUS OF SCHEDULE-INDUCED POLYDIPSIA.

An experimental investigation of the temporal locus of drinking, an examination of responding to a tube that did not permit drinking, and the results of a choice experiment between these two topographies. Some considerations of the adjustive aspects of polydipsia, and the relationship of the experimental results to methodological considerations.

C O N T E N T S

CHAPTER

V RESPONSES TO NON-CONTINGENT FOOD DELIVERY IN THE FERRET: AN ASPECT OF THE SPECIES GENERALITY ISSUE.

A critical review of the literature on the species - generality of schedule-induced polydipsia, some attempts to obtain this behaviour in ferrets, an attempt to demonstrate schedule-induced wheel-running in this species and considerations of the negative findings from these experiments.

VI RESPONSES TO NON-CONTINGENT FOOD DELIVERY: A COMPARATIVE OBSERVATIONAL ANALYSIS.

An introduction to methodological problems of observational techniques of study, a system of categorising the behaviour of rats and ferrets, a comparative observational experiment on these two species and a discussion of the differences in results.

VII DISCUSSION AND CONCLUSIONS.

A brief overview of schedule-induced polydipsia, its temporal locus and species-generality, the responding to the licking tube, and the significance of the research to theories of adjunctive behaviour.

REFERENCES

APPENDIX:

I ANIMAL BEHAVIOUR: SOME CURRENT ISSUES AND PROBLEMS.

An essay that selectively examines some aspects of the study of animal behaviour, a short historical overview, origins and issues in comparative psychology, behaviourism, and ethology, and a brief assessment of current viewpoints, with references.

II OF RATS AND FERRETS.

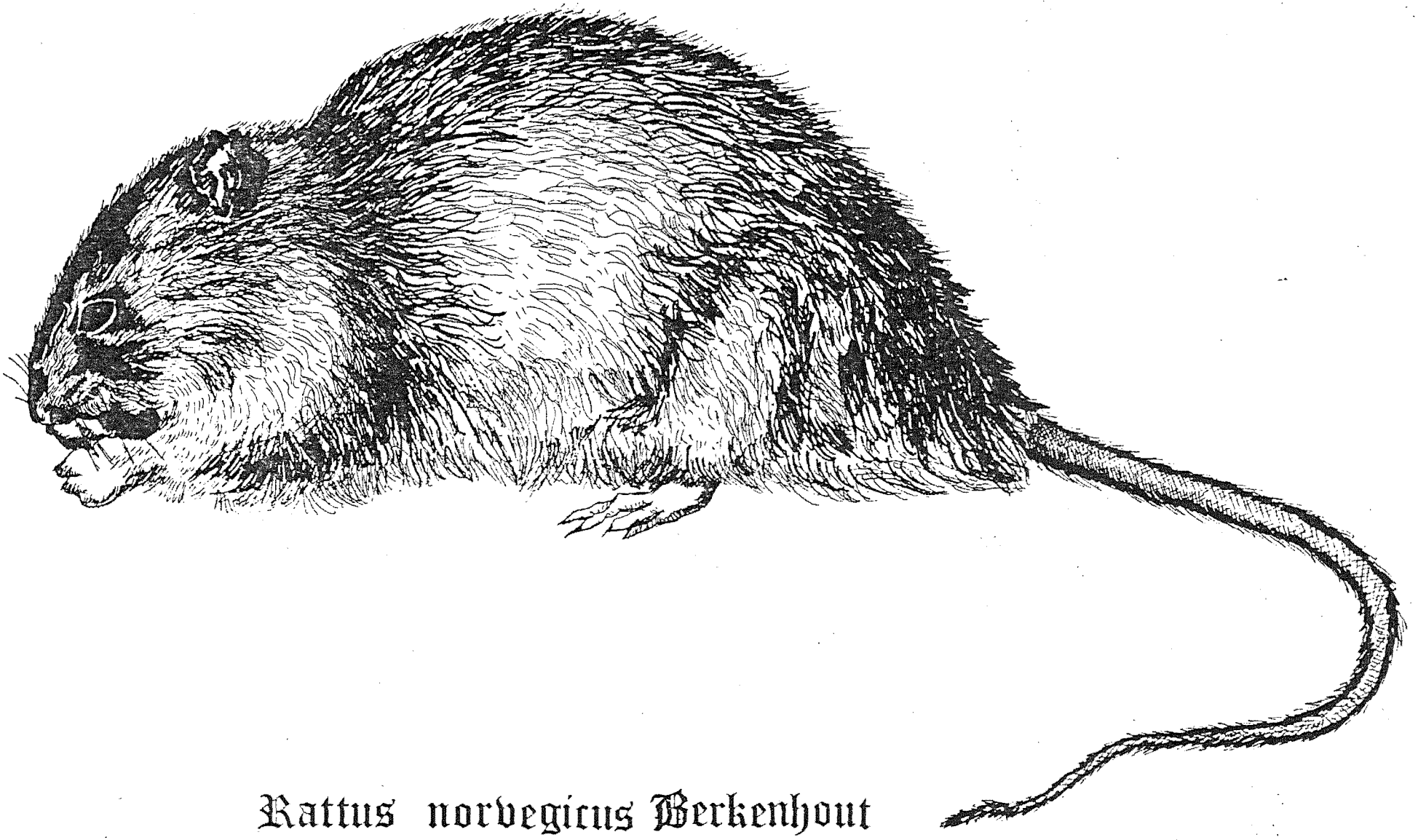
A brief review of the biology and behavioural literature pertaining to these two species, with references.

III A DESCRIPTION OF THE EXPERIMENTAL APPARATUS USED

The equipment used, its specifications, dimensions and operation.

IV. THE HOUSING AND DIET OF THE SUBJECTS.

Notes on the husbandry of the rats and ferrets, and specifications of their diet.



Rattus norvegicus Berkenhout

Mustela putorius Linnaeus hybrid

PROLOGUE

The behaviour of animals is greatly influenced by the ecological niches they occupy. The rat typifies the omnivorous mode of existence, exploiting a range of food sources, and being exploited as prey itself. The ferret exemplifies the carnivorous existence, enjoying the relative luxury of an enriched protein diet and few predators.

The differing modes by which these two species exist is reflected in their behaviour within the laboratory situation. It is to these differences in behaviour that the experimental questions in this thesis are addressed.

C H A P T E R 1

I N T R O D U C T I O N

In recent years the study of animal behaviour has undergone a number of changes. These relate to several issues, and reflect a changing awareness amongst those who study animals that many approaches in the past led to insularity and a lack of dialogue. Factional isolation seems a byproduct of the way the various approaches to the subject developed, and despite numerous polemics and researches one of the most influential challenges arose out of findings that were obtained from a completely non-academic source: commercial enterprise.

In 1951, Breland and Breland reported their experiences in the field of applied animal behavour, and optimistically described the application of operant conditioning techniques to modify the behaviour of various species for commercial purposes. Their results indicated that laboratory-based principles readily generalised to behavioural control in a non-laboratory setting.

> "We can apply to our training the data of comparative psychology, utilising new tricks, new animals. We can turn our multiple units - 200 "Clever Hanses" instead of one. Furthermore, the systematic nature of the theory puts us in a position to advance to new and

more elaborate behaviour patterns,
to predict results and forestall
difficulties." (Breland and Breland,
1951).

In subsequent publications they confirmed the financial viability of animal training in commercial enterprise, but they also noted frequent and disconcerting failures amongst their trained subjects, which might be summarised as,

"Sometimes animals do not do what they
were taught to do."

These aberrant subjects developed behaviour patterns unrelated to those they were taught to perform, often to the extent that the subject had to be removed from the exhibition setting as the behaviours were disruptive; examples of these are summarised in Breland and Breland (1961). In all instances the animals performed the trained responses to perfection, yet they developed alternate patterns of behaviour that often led to the total exclusion of the programmed reinforcement. Not only did the intrusive behaviour require more effort and was more time consuming; it also increased the deprivation effects upon the animal, which in turn increased the level of intrusive behaviour.

This behaviour was accounted for in terms of "instinctive drift", which implied the principle,

"where an animal has a strong instinctive
behaviourin the area of a conditioned
response, after continued running the
organism will drift toward the instinctive

> behaviour to the detriment of the conditioned behaviour, and even to the delay or preclusion of reinforcement ..... It seems obvious that these animals are trapped by strongly instinctive behaviours, and clearly we have a demonstration of the prepotency of such behaviour patterns over those that have been conditioned." (Breland and Breland, 1961).

The implications of this statement run contrary to some of the basic assumptions of Behaviourism, namely that species differences are relatively unimportant as all responses are equally conditionable to all stimuli. As will be discussed later, Seligman (1970, 1972) has termed this assumption "the equipotentiality premise," citing Pavlov (1927, 1928), Estes (1959) and Skinner (1938) as theorists who hold this view.

The Breland's publications did not purport to justify a theoretical viewpoint; rather they were motivated by pragmatic commercial necessity: they did not defend any thesis regarding the operant conditionability of a range of species, but were forced to accept the limitations of this technique:

> "After fourteen years of continuous conditioning and observation of thousands of animals, it is our reluctant conclusion that the behaviour of any species cannot be adequately understood, predicted,

> or controlled without knowledge of its instinctive patterns, evolutionary history, and ecological niche." (Breland and Breland 1961).

This viewpoint essentially restates Darwin's position nearly a century earlier, in which behavioural and morphological adaptations were seen as complementary evolutionary processes:

> "In his theory of natural selection Darwin recognises the importance of variation and of organic diversity. The history of life reflects as much an adaptive radiation, with behaviour of different kinds having evolved in different ecological situations, as it does a progressive elaboration of better organisms with nervous systems increasingly like our own." (Ghiselin, 1973).

Since the publication of the Breland's work a number of issues have arisen that challenge traditional psychological approaches to animal behaviour, and which directly relate to the views contained in these latter quotations:

(A) Superstition:

The traditional operant view that animals will develop sterotypical behaviour when presented with reinforcement without regard to what they were doing received strong criticism from Staddon and Simmelhag

(1971). They questioned the simple learning theory premises upon which this phenomenon rested, arriving instead at,

> "an interpretation of behavioural change in terms of interaction and competition among tendencies to action according to principles evolved in phylogeny."

(B) Adjunctive Behaviour:

Arising out of Falk's (1969, 1971) studies on schedule-induced polydipsia, was an awareness that a variety of behaviours occur as adjuncts to specific behavioural events, that these appeared similar to the "displacement activities" of ethological research, and that these adjunctive behaviours were not explicable in purely behaviouristic terms, but contained a degree of species - typicality.

(C) Autoshaping:

Studies by Brown and Jenkins (1968) demonstrated that the simple temporal pairing of lighting a key and following it with the presentation of grain will result in a pigeon acquiring a key-pecking response, even when it has no effect on producing grain. Williams and Williams (1969) further extended this phenomenon with the discovery that key-pecking will persist even when it actually prevents the delivery of reinforcement, whilst Moore (1972) demonstrated that the actual pecking behaviour resembles the more appropriate consummatory response pattern when water or

grain are presented.

(D) Avoidance Learning:

Bolles (1970) presented evidence to support the view that some avoidance responses are difficult to train, whilst others are relatively easy, and that these differences are accountable in terms of "species-specific defence reactions." He criticised the limitations that preoccupations of traditional theory imposed upon this type of learning, noting,

> "These preoccupations have not really advanced our understanding of how such extensions occur, how other, more natural R_as are learned, *or for that matter how animals survive in nature."* (Italics mine).

(E) Behaviour Epigenetics:

Kuo (1967) challenged traditional approaches to the study of behaviour as being too limited and simplistic in outlook, and proposed an alternate view in which the epigenseis of behaviour was seen as the main goal of study. His views embodied both behaviouristic and naturalistic data, and the combination of which served,

> ".....to obtain a comprehensive picture of the behavioural repetoire of the individual and its causal factors from stage to stage during development; and to explore the potentials and

> limitations of new behaviour patterns ("behavioural neo-phenotypes") that are not commonly observed or do not exist in "nature" so as to predict or control the evolution of behaviour in the future" (Kuo, 1967, p26)

(F) Preparedness:

Seligman (1970, 1972) suggested that all events are not equally associable, but that some events are easily so (prepared responses), some are difficult (unprepared) and some are impossible (contraprepared). This approach was further extended by Hinde et al (1973) in an examination of the numerous biological constraints on learning.

In all these instances the issue revolves around the relative importance of biological factors in animal behaviour, and corresponds to a major re-examination of approaches to this subject. These changes relate to comparative psychology being criticised on methodological grounds (eg. Beach, 1950; Hodos and Campbell, 1969; Lockhard, 1971), to behaviourism being challenged on theoretical grounds (Breland and Breland, 1961; Seligman 1970), and to the influence of ethology which emphasised evolutionary and ecological considerations (Lorenz 1954; Hinde, 1966). Having passed through a period of polemics and assiduous debate in the 50's and mid 60's, the study of animal behaviour now appears to be in a state of re-organisation and fruitful growth - analogous to the "hybrid vigour" of genetics - as differing emphases and methodologies are grafted onto the various phenomena studied.

The phenomenon studied in this thesis, schedule-induced polydipsia, is one of a number of behaviours that can be studied from several combined methodological viewpoints. The phenomenon is laboratory-based, occurring in an experimental environment where most physical variables are known and controlled, leaving the organismic (i.e. phylogenetic) variables to express themselves. It is comparable to "displacement activities" which are well recorded in ethological research, and to which naturalistic observations closely relate, and is measureable both by the automatic devices of experimental psychology (e.g. drinkometer records, liquid volume intakes, temporal distribution of responses), and by observational methods (which reveal patterning and sequences of responses).

Due to the nature of the experimental procedure adopted in the research reported herein learning differences between species were minimised (since the subject had only to learn the signal for, and the spatial location of, food delivery), which in turn provided a valid methodological justification for the use of the comparative approach. As is discussed in Appendix 1, the comparative approach examines both similarities and differences between the groups being studied. In this instance, the dissimilar results provide a useful basis to draw conclusions upon, and to suggest further hypotheses. The species selected for study were from differing ecological niches, and consequently exhibted different patterns of eating and drinking behaviour. The development of schedule-induced polydipsia in the omnivorous rat is investigated in the light of species-related influences , whilst the failure to obtain this phenomenon

in the carnivorous ferret is considered from both a species-specific and a methodological viewpoint.

C H A P T E R T W O

SCHEDULE-INDUCED POLYDIPSIA

A: INTRODUCTION.

B: DISPLACEMENT ACTIVITIES AND ADJUNCTIVE BEHAVIOUR.

C. SCHEDULE-INDUCED POLYDIPSIA: SOME IMPORTANT PARAMETERS.

1. Deprivation Level.
2. Response-Contingency.
3. Interval of Food Delivery.
4. Type of Food.

D: EXPLANATORY ATTEMPTS.

1. Physiological Factors.
2. Experimental Environment Artifacts.
3. Adventitious Reinforcement.
4. Dry-mouth Theory.
5. Timing Behaviour.
6. Interim Activities.
7. Arousal Concepts.

E: SOME TEMPORAL CONSIDERATIONS.

F: AN EXPERIMENTAL DIRECTION.

C H A P T E R T W O

SCHEDULE-INDUCED POLYDIPSIA.

(A) Introduction.

Since Falks' initial report in 1961, schedule-induced polydipsia has been a topic of experimental investigation and theoretical speculation. The speculation regarding its causation has been a legacy of the unexpected nature of its discovery, as Falk stumbled upon this behaviour during investigations on reinforcement-schedule effects in food deprived rats. Its discovery parallels Skinner's early investigations which led him to his formulations on the operant control of behaviour, by a process which he called the "principle of serendipity",

> "the art of finding one thing while looking for something else" (Skinner, 1959).

Falk has discussed the unexpected nature of this discovery thus:

> "About a decade ago, a rather fortuitious experimental arrangement enabled me to happen upon the phenomenon of schedule-induced polydipsia. Fortunately, I had already worked on the control of fluid intake in the rat and from such a context knew the production of polydipsia as a food-schedule by-product was not only an unusual one - it was an outrightly

> absurd one. It was absurd because heating a large quantity of room temperature water to body heat and expelling it as copious urine is wasteful for an animal already pressed for energy stores. It is absurd for an animal to drink itself into a dilutional hyponatremia bordering on water intoxication. But perhaps most absurd was not the lack of a metabolic or patho-regulatory reason for polydipsia, but the lack of an acceptable behavioural account" (Falk, 1972).

This quotation emphasises the most dramatic aspect of polydipsia; an intake of water far in excess of the normal daily requirements of the animal.

The essential procedures to produce it are that the subjects be food deprived, that small portions of food are delivered intermittently, and that a source of water is freely available. In this situation Falk noted that his subjects drank nearly 350% of their pre-experimental 24 hour water intake level in 3.17 hours ie. the animals were drinking nearly half of their body weight in liquid in a comparatively short time. Since the subjects were in a state of food deprivation (70 - 80 percent free - feeding weight), this water intake was unexpectedly large, as the normal water intake in food deprived rats is invariably depressed below free-feeding weight levels (Adolph, 1947; Bolles, 1961; Kutscher, 1969). The animals rapidly developed a pattern of bar-pressing until the reinforcement was delivered, followed by the con-

sumption of about 0.5 mls of water, and a return to bar pressing.

The level of water consumption was markedly greater than levels obtained by other methods of experimentally-induced drinking:

> "Such a phenomenon is stange and unprecedented, for the animals are drinking approximately one-half their body weight in a few hours. Water deprivation, heat stress, or osmotic-loading techniques do not approach comparable stimulation of water intake. Under normal laboratory maintenance conditions, daily water intake levels remain rather constant, and even strong facilitating stimuli induce only moderate increases" (Falk, 1969).

As will be reviewed later in this chapter, schedule-induced polydipsia was also obtained on a variety of reinforcement schedules, on delivery schedules that did not require a bar-press response, and indeed on totally non-contingent food delivery schedules. The phenomenon was confirmed in other strains of rats, (Falk, 1972), as well as other species: rhesus monkey (Schuster & Woods, 1966; Porter and Kenshalo, 1974), chimpanzee (Keller, cited Falk, 1972), pigeon (Shanab & Peterson, 1969), mouse (Palfai, Kutcher and Symons, 1971). It bears a close relationship to other schedule-induced phenomenon such as schedule-induced aggression (Ulrich & Azrin, 1962), schedule-induced pica (Villareal, 1967), schedule-induced wheel-running

(Levitsky & Collier, 1968), and schedule-induced air licking (Mendelson & Chillag, 1970). This close relationship led Falk to label such phenomena "adjunctive behaviours":

> "The experimental design is simple, yet the behavioural effect is strong and durable. Sidman (1960) has wisely pointed out that: "whenever a simple operation is found to exert a powerful behavioural effect, we may suspect that the phenomenon can be widely generalised." I have indicated previously that another behavioural phenomenon, extinction-induced aggression reported by Azrin and his associates, stands in the same relation as polydipsia to its generating schedule (Falk, 1966a 1966b). I suggested that when certain schedules induce extra, concurrent phenomenon strong enough to sustain scheduled behaviour in their own right, that these phenomenon be called "adjunctive behaviours" (Falk, 1972).

In his 1969 article, Falk pointed to the similarities between schedule-induced polydipsia and the "displacement activities" which comprised a substantial part of ethological research in the 1940's and 50's. He further elaborated these arguments in his 1972 paper, in which he concluded that such activities (ie. adjunctive and displacement behaviours) had an adaptive value in that they,

> ....."increase the organisms' probability of responding in strength to other

> possibilities in the environment context by increasing the gain or operant units receiving relatively low, but appreciable, facilitation from current environmental stimuli."

It would seem that this relationship between the schedule-induced phenomenon and displacement has a major bearing on the understanding of adjunctive behaviours at the behavioural/ethological level, and perhaps on the physiological.

(B) Displacement Activities and Adjunctive Behaviour.

> "The term "displacement activity" implies that the behaviour is misplaced and occurs outside its proper context. But recent research has revealed that the behaviour is a function, not only of the conflict or thwarting condition, but also of stimulus variables which normally operate in its control. This is one reason for preferring the term "adjunctive behaviour", for it implies only that the observed behaviour occurs as an adjunct to another behaviour situation without evaluating the appropriateness or adjustive gains of that additional behaviour" (Falk, 1969).

By adopting the term adjunctive behaviour, Falk has circumvented the problem of "irrelevancy" implicit in thinking on displacement activities, which have been defined as,

"behaviours occurring out of their characteristic motivational context and in the midst of conflict and thwarting situations" (Zeigler, 1964).

As McFarland (1966) has noted, these behaviour patterns were described as long ago as 1914, although it was Tinbergen and Kortland in 1940 who did the first causal analysis of the phenomenon. Originally they were labelled "substitute activities" (Kirkman, 1937), the term "displacement activities" being a later choice (Armstrong; 1947, 1950). This latter term is now the preferred rubric, and arises largely out of the translational equivalence between English and the German word Ubersrungbewegungen which refers to the "sparking over" of motivational energies belonging to one instinct, to another. The features of these behaviours were noted by Tinbergen (1952) as:

1. Displacement activities are recognisably similar to, or derived from, motor patterns which are normal for the species.
2. The movements shown appear 'irrelevant', entirely out of context with the behaviour immediately preceeding or following them.
3. A displacement activity seems to appear when an activated drive is denied discharge through its own consummatory act(s)."

Clearly, 'irrelvant' implies some formulation by which the criteria of relevancy are judged, or else these statements are liable to criticism on the grounds of teleology, utilitarianism, and anthropomorphism.

McFarland has eloquently discussed this issue of relevancy noting that the use of the term relevant may be concerned with either functional or causal aspects of behaviour, when used with reference to some formulation or model.

> "When an activity is observed in circumstances which are not in agreement with the accepted formulation, it may be called irrelevant" (McFarland, 1966).

He discusses varying approaches and concludes that causal criteria can only reflect the theoretical model used to account for the behaviour, which is reasonable, since the animal engaging in the displacement activity must be responding to some causal influence by the very existence of the behaviour. He concludes,

> "It is argued that it is impossible for an activity to be truly irrelevant causally, but it is possible for it to be functionally irrelevant, either in the sense that it has no survival value, which, however, cannot be proved; or in the sense that the activity fails to fulfill its normal short-term function".

The classical ethological explanation of displacement activities related to the energy-based motivational models of Lorenz (1937, 1950) and Tinbergen (1940, 1951), in which a build up of motivational energy discharging into the next appropriate behavioural pathway was assumed to account for the phenomenon.

> "Each of these specific patterns of behaviour was assumed to be organised around and motivated by energy associated with a particular center, presumably localisable somewhere in the central nervous system. Tinbergen further elaborated this model by supposing that a surplus of energy in one center, if blocked or prevented from being discharged, or in the absence of the appropriate releaser, could "spark over" to other centers, even centers controlling quite unrelated behaviours (Tinbergen, 1940, 1951). It had been noted by a number of ethologists that instinctive behaviour patterns often occur out of context, most typically in situations in which the behaviour of another instinctive pattern is blocked or frustrated in some way" (Bolles, 1967, p103).

Although there were psychological postulations of energy models of motivation (eg. Freud, 1915; McDougall, 1932; Cannon, 1918; Warden, *et al*, 1931; Tolman, 1926) the ethological models received the greatest criticism, largely because they were based upon naturalistic data and were accordingly bereft of empirical validation: for a review of these criticisms see Lehrman (1953), Hinde, (1959, 1960), and Zeigler (1964).

> "Tinbergen's theoretical account of displacement had a great deal of appeal, it was simple and elegant, but it did not foster any empirical attack upon the problems presented by the

> displacement phenomenon. Hinde and Zeigler have both suggested that Tinbergen's energy model was too pat, too facile - it discouraged an experimental analysis of behaviour. Like McDougall's analysis of instinctive behaviour a generation before, it proposed answers when questions might have been more valuable" (Bolles, 1967).

Amongst psychological considerations of displacement, the contribution of Bindra (1959) seems most apposite, especially in regard to the similarity between displacement and adjunctive behaviours. He noted that displacement can be accounted for in terms of three main features,

1. An increase in the level of arousal of the animal bought about by the obstructing event (ie the conflicting event, or deprivation effects).
2. The relative habit strengths of various activities within the repertoire of the animal (ie the prepotency of response concept).
3. The nature of the sensory cues provided by the altered stimulus situation (ie those stimulus objects and events within the current environment which act as cues to evoke the specific behaviours).

As will be discussed later, these features seem to apply well to situations producing schedule-induced polydipsia.

Beyond the classic Lorenz-Tinbergen model of displacement, alternative accounts have appeared, which have some relevance. For reviews of some of these see: Van Iersel and Bol (1958), Sevenster (1961), Rowell (1961), Von Holst and Mittelstaedt (1950, 1954), Bastock, Morris and Moynihan (1953), and McFarland (1966b, 1970b, 1971, 1974).

In comparing displacement activities and polydipsia, it becomes apparent that a number of similarities exist, which indicate the possibility that they share a similar process, although one is evident in the natural environment, and the other peculiar to the laboratory.

> "Thus, displacement activities are described as occurring in situations where an animal under high drive conditions is engaged in a phase of the consummatory behaviour and for some reason is prevented from continuing this behaviour. These are also the conditions producing adjunctive behaviours: a lean animal engaged in eating is prevented from continuing this behaviour by the intermittence imposed by the feeding schedule..... In both adjunctive behaviour and displacement activity situations, the interruption of a consummatory behaviour in an intensely motivated animal induces the occurrence of another behaviour immediately following the interruption, which is facilitated by environmental stimuli" (Falk, 1972).

(C) Schedule-induced Polydipsia: Some Important Parameters.

The parameters influencing schedule-induced polydipsia are well reviewed : see Falk (1969, 1971, 1972), Segal (1972), Hawkins, Schrot, Githens & Everett (1972). These papers discuss the influence of degree of deprivation, schedules of reinforcement, magnitude of reinforcement, type of food, effects of liquids other than water and the proximal events controlling this behaviour. Consideration of specific paramenters has been restricted herein to those that have direct relevance to the research reported in this thesis.

1. Deprivation Level:

Falk (1969) systematically decreased the level of deprivation in polydipsic rats until the animals regained their free-feeding body weights, and found a marked attenuation in the level of polydipsia after the animals attained 95% free-feeding weight. The concurrent bar-press contingency in this experiment was relatively unaffected by a decrease in deprivation level, which indicates that the adjunctive behaviour was under the control of factors other than operant response rates and is directly influenced by the level of deprivation. Falk cites instances where adjunctive behaviours (other than polydipsia) reveal a similar relationship (eg. schedule-induced air-licking (Mendelson and Chillag), schedule-induced aggression (Azrin *et al* 1966).

> "Even though the consummatory activity occurs unfailingly and the appetitive sequence (operant pattern) remains at its customary rate, the operations must define a rather intense deprivation state in order for adjunctive behaviour to be induced in its fully-developed, exagerated form" (Falk, 1972).

This information is crucial when interspecies comparisons are attempted, since the motivational states of deprivation must be as equivalent as possible, and it may be impossible to apply the 80% free-feeding weight criterion (as used with rats and pigeons) to other species which may not tolerate such levels of deprivation. Thus preliminary studies of motivational levels are necessary when using relatively "novel" species, such as the ferret, to ensure that the subjects' are indeed in "a rather intense deprivation state". It can be conjectured that species such as voles and shrews may not be able to tolerate intense food deprivation (along with the attendant heat loss due to schedule-induced polydipsia) since they maintain a tenuous balance between activity and feeding, and alternative behaviours might have to be manipulated in order to demonstrate adjunctive behaviour. Similarly a herbivore, such as the rabbit, may present difficulties with respect to the considerable storage of low-caloric cellulose in the caecum which renders conventional deprivation-level manipulations difficult.

2. Response-Contingency:

As early as 1961 Falk had demonstrated that the omission of the bar-press contingency for food delivery still produced a comparable amount of polydipsia. This observation disproved the possibility that schedule-induced polydipsia was a displacement from the momentarily low probability of bar pressing to another behavioural activity. Since this study, numerous papers have reported the reliable demonstration of schedule-induced polydipsia using non-contingent schedules (usually fixed-time schedules) eg. Segal, Oden and Deadwyler (1965); Segal (1965); Reynierse (1966); Segal and Oden (1969); Toates (1971); Wayner and Greenberg (1973).

Schaeffer, Diehl and Salzberg (1966) found that free fixed-time food schedules could concurrently maintain polydipsia and a bar-pressing response (although the bar-pressing response had no influence on food-delivery). They interpreted these results as evidence that adventitious correlations between bar-pressing and food-delivery could occur, since the bar-pressing preceded the delivery of food in their study, while the drinking occurred as a post-pellet event. They proposed that this possibility also suggested that an adventitious correlation between drinking and food-delivery might occasionally occur; which subsequently was reported by Schaffer and Salzberg (1967) in an atypical case (this report will have bearing on the next section dealing with explanations of schedule-induced polydipsia). Wayner and Greenberg (1973) also reported bar-pressing occurring in a free fixed-time

schedule, but noted that this adjunctive bar-pressing "followed the same time related function as licking and water consumption". This study does not acknowledge the two previously cited, nor does it provide quantified distributions of either the licking or bar-pressing behaviours, but it does propose that the bar-pressing behaviour can also be an adjunctive behaviour. Overall, these studies indicate that explicit dependancy between the operant response and pellet delivery is not a crucial determinant in schedule-induced polydipsia, and that the operant responses themselves may develop into adjunctive behaviours.

The use of non-contingent schedules of food delivery provides the simplest experimental manipulation to produce schedule-induced polydipsia, since the phenomenon is relatively uncontaminated by learning factors: this is important when comparisons between different species are attempted. Thus any given subject has only to learn where food will be delivered, what signals indicate its arrival, and that this delivery of food is intermittent. As some species do not readily acquire the bar-press response, inter-species comparisons can be restricted when this contingency is used: this problem is avoided with non-contingent schedules of food delivery.

3. Interval of Food Delivery:

Falk (1966b) systematically varied the interval between food delivery (using a fixed-interval schedule) from 2 seconds to 300 seconds and found that the maximum

level of polydipsia was attained at about 180 seconds in rats, whereafter the polydipsia declined rapidly. Subsequent studies by Segal (1965); Hawkins (1967); Falk (1969); Flory (1969c) and Hawkins et al (1972) confirmed this bitonic relationship: for an extended discussion see Falk (1972).

This bitonic relationship between the interval of of food delivery and magnitude of polydipsia has an important relevance where comparisons between adjunctive behaviour in different species are attempted, since an optimum interval of food delivery must be adopted if adjunctive behaviours of a reliable magnitude are to be generated, and this interval may vary from species to species.

4. Type of Food:

Early studies by Stein (1964) and Stricker and Adair (1966) indicated marked attenuation of polydipsia when food pellets were substituted with milk portions and wesson oil respectively. Falk (1967), however, obtained high levels of polydipsia using liquid-monkey diet, an observation later supported by Hawkins *et al* (1972). These later researchers were unable to obtain levels of polydipsia comparable with Falk's and they noted that the polydipsia appeared to have a slow period of development. They concluded that the type of food used had "a considerable influence on the development of polydipsic drinking". These studies were primarily concerned with the differences between liquid and dry food diets, in line with theoretical speculations as to the role of a "dry mouth" as a causal factor in polydipsia.

Alternative studies have varied the nutritive content of dry food in order to examine the role of caloric factors. Freed (1971) evaluated the degree of polydipsia against nutritive content of food pellets, finding that, "the mean volume of water ingested decreased with decreased nutritive content of the pellets"; with saccharin-sweetened nonnutritive pellets producing negligible drinking, and 100% nutritive pellets providing polydipsia at an expected level. This study is equivocal however, since the 100% nutritive pellets used were 45 mg Noyes Laboratory Animal Food pellets, which were substituted randomly half of the time with non-nutritive food pellets in the 50% nutritive condition. The use of Noyes Laboratory Animal Food pellets was subject to criticism by Christian and Schaffer (1973a, 1973b), with respect to the presence of 7.5% glucose in these pellets, which along with sucrose (in other types of pellet) is known to attenuate polydipsia - eg. Falk (1967), Segal *et al* (1965), Burks et al (1967). Christian & Schaeffer concluded that,

> ".....the presence of any sugar in a Noyes pellet, whether it is glucose or sucrose, produces reduced fluid intakes relative to those that are obtained from Noyes pellets that contain no sugar".

These studies indicate the importance of oral and palatability factors in polydipsia, although the phenomenon appears to be reliable and relatively resistance to some aversive factors. The adulteration of drinking liquid quinine (a normally aversive substance) fails to abolish

schedule-induced polydipsia (Segal and Deadwyler, 1965). When the drinking liquid is adulterated with saccharin, and then paired with ionising radiation, repeated pairings were necessary to reduce the level of polydipsic behaviour (Roll, Schaeffer and Smith, 1969), although this procedure normally produces a marked aversion to saccharin in thirst motivated rats with one pairing (Garcia and Kimeldorf, 1960; Garcia, Kimeldorf and Hunt 1961).

When comparative evaluations between species are attempted, palatibility and oral factors may present a source of confounding of results. To some extent, ecological factors (ie whether the subjects are carnivores or herbivores etc), may override simple control for these factors, which suggests the need for care in the choice of food and of liquids to be consumed.

(D) Explanatory Attempts.

From the earliest reports of schedule-induced polydipsia, there have been several attempts to explain the phenomenon, often at the most simple level, such that one group of authors were moved to remark:

> "An examination of the relevant polydipsia literature led us to conclude that much of the rhetoric surrounding the theoretical arguments was superfluous and incomplete, being based primarily on anecdotes and unsound predictions, with the primary cause of confusion being the lack of general information about the phenomenon". (Hawkins

et al, 1972).

In the same volume, Falk commented that:

> "Thus a decade of research has yielded no traditional physiological or behavioural explanation for schedule-induced polydipsia. Attempts to account for the behaviour as an 'emotional' side-effect of schedules, or as the animal's way of producing 'emotional pacification' are not necessarily wrong, but they are largely untestable notions".

It is not intended to provide an expanded discussion of many of these accounts of the phenomenon: for a review see Falk (1969). However, a brief consideration of some accounts is necessary in order to relate to some more recent suggestions.

1. Physiological Factors:

Considerable evidence has shown that there is no simple physiological explanation for the phenomenon on the grounds of,

(i) the food deprivation regime presented to the subject (eg. Falk, 1967).

(ii) nephrogenic diabetes insipidus (Stricker and Adair 1966).

(iii) de facto water deprivation (Falk, 1969).

The physiological evidence indicates that the subjects are in a state of overhydration, as measured by plasma and muscle water, hemotocrit, and plasma protein post session (Stricker and Adair, 1966).

2. Experimental Environment Artifacts:

Simple control procedures have eliminated such explanations as,

(i) conditioned reinforcing and discriminative properties of the experimental equipment.

(ii) taste phosgenes from drinkometer currents.

(iii) type of liquid dispenser.

(iv) operant response situation demands.

3. Adventitious Reinforcement:

Based upon Skinners' (1948) concept of "superstitious behaviour", schedule-induced polydipsia was considered as an example of adventitious reinforcement by Clark, (1962), and by Segal (1965). The polydipsic behaviour develops out of an adventitious pairing of drinking behaviour just prior to food delivery, thereby setting up a chain of behaviour. However, this view seems oversimplified, and is untenable on a number of grounds,

(i) superstition is idiosyncratic and unstable, its' response topography changes over time: polydipsia is stable and relatively invariant.

(ii) superstitious drinking would tend to precede eating when the probability of reinforcement is high: polydipsia is generally a post-pellet phenomenon occurring soon after food delivery. (Stein, 1964; Falk, 1969).

(iii) the imposition of a "change over delay" (COD), which is effective in eliminating adventitous responding does not attenuate polydipsia

(Falk, 1964; Segal and Oden, 1969).

(iv) superstitious behaviour requires a relatively short interval between food deliveries to develop as long delays (in the order of 60-100 seconds) do not reliably produce this behaviour : schedule-induced polydipsia is reliably produced over long inter-food intervals (Falk, 1969).

4. Dry-Mouth Theory:

Stein (1964) proposed that the dry food pellets used in schedule-induced polydipsia made the subjects thirsty, and that they then drank to alleviate this state. This view was further supported by Teitelbaum (1966), who speculated as to the abolishion of polydipsia if the subjects were given liquid food portions, or if prehydrated. This possibility was discounted by Falk (1967, 1969) who used liquid-monkey diet, and preloading of the oesphagus with water, and still obtained strong polydipsia. Lotter, Wood and Vasselli (1973) also presented a dry-mouth theory, although they don't seem to have been able to counter the evidence to the contrary cited above.

5. Timing Behaviour:

Segal and Holloway (1963) suggested that the subjects were using water drinking as a means of "pacing their response rate" on a DRL 20 schedule, and hence timing themselves on mediating response sequences such as drinking. This view was extended by Segal and Deadwyler (1965) who proposed that drinking was precipitated by thirst (from dry

pellets) and continued as it provided the subjects with "timing cues derived from taste and quantity consumed". However, this view is unacceptable, since VI 60, FR 30 and non-contingent VI 60 schedules produce polydipsia although "there is no regular, scheduled duration that any "timing behaviour" is required to time" (Falk, 1969). Segal appreciated this point, and further countered her own proposal by noting that "polydipsia occurs even when a *reinforced* alternate response (bar pressing on a variable-ratio schedule) is available" (Segal and Oden, 1969). The role of timing factors has since been re-evaluated in another approach, which embodies more sophisticated formulations, rather than the abovementioned simplified accounts, and will be considered separately.

6. Interim Activities:

Skinner's classic (1948) experiment of "superstition" was re-examined by Staddon and Simmelhag (1971) in the light of more recent thinking that challenged the traditional Skinnerian analysis. They cited both schedule-induced polydipsia and "misbehaviour" as examples of phenomena that may involve processes that suggest a reinterpretation in,

> "terms of interaction and competition among tendencies to action according to principles evolved in phylogeny".

By extending the classical Skinnerian experiment they elucidated the development of two kinds of behaviour at asymptote, which they termed *interim activities* and

terminal response. The *terminal response* is seen as being a discriminated operant which is "restricted to periods of relatively high reinforcement probability," ie that period in the experiment just before food delivery. *Interim activities* occur after periods of food delivery (when the probability of reinforcement is zero) and are interpreted as interactions amongst motivational systems which express themselves as appetitive - like behaviours. Examples of these phenomena include adjunctive behaviours, displacement activities, redirection, and "vacuum" activities (see section B).

Interim activities are influenced by the availability of appropriate stimuli ("goal objects" in ethological terminology) such that variable and undirected interim activities become ordered in the presence of these stimuli, eg. polydipsia occurs when drinking tubes are available, pica in the presence of woodblocks etc. These activities are assumed to have an adaptive significance in that they permit the animal to break away from a particular behaviour, and to engage in other behaviours when that behaviour no longer is gainful in combining these formulations of interim activities and terminal response, Staddon and Simmelhag conclude that,

> ".....the most distinctive thing about living creatures is the balance they maintain amount a number of tendencies to action, each one adaptive, yet each destructive if pursued to the exclusion of others."

Thus their model attempts to explain polydipsia (and adjunctive behaviours generally) in terms of a biological process that draws a parallel between these behaviours and (the more natural) displacement activities in a similar manner to Falk (1972), and contrasts with the timing behaviour account of polydipsia (which sees polydipsia as timing behaviour *per se*). This approach views polydipsia as one of a number of behaviours that assist in helping to budget the organisms' time more efficiently.

> "Evolution is notoriously opportunistic in the sense that adaptation is achieved by whatever structural or functional means happen to be available. (In the present case) we suggest that the means for insuring that the animal will not linger in the vicinity of food (or other reinforcers) at times when it is not available may be provided by the facilitation of drives other then the blocked one". (Staddon and Simmelhag, p38).

This account is significant in that it combines methodological direction with theoretical (evolutionary) considerations, and as will be discussed later, complements other formulations on this topic.

7. Arousal Concepts:

Wayner, (1970, 1972, 1974) proposed an account for adjunctive behaviours based upon "arousal factors within the C.N.S.; specifically, the lateral hypothalamus (L.H.). Schedule-induced polydipsia (and adjunctive behaviours

generally) result from stimulation of the L.H., which is brought about by the influences of physiological deprivation and the schedule of reinforcement used. Stimulation of the L.H. then produces a state of arousal and activation within the organism, which manifests itself as adjunctive behaviour, according to the presence of appropriate stimuli within the immediate environment.

This theory relates to previous formulations on non-specific "arousal", "activation" or "drive", (eg. Hebb, 1955; Berlyne, 1960; Duffy, 1962; Bindra, 1969;) in which "arousal" is seen to function as a general activator of behaviours. Arousal concepts have also been applied to accounts for displacement activities (see section B); for example, Bindra (1959) specified an increase in arousal as one of the major factors of importance in his analysis of this phenomenon.

Wayner interprets the fact that adjunctive behaviours develop according to the presence of appropriate stimuli in the environment as a corollory to studies on electrical stimulation of the L.H. which indicate that,

> "The type of behaviour evoked by lateral hypothalamic electric stimulation depends upon the environmental stimuli available during brain stimulation. By careful manipulation of the availability of environmental stimuli it is possible to switch the type of behaviour evoked: for example, from eating to drinking, through

the same electrodes without alteration
of the stimulus current". (Wayner, 1970).

This view has support from a number of studies, in particular those of Glickman and Schiff (1967), Valenstein, Cox and Kakolewski (1969, 1970), White, Wayner and Cott (1970) and Glickman (1973). That the stimulus-bound aspect of adjunctive behaviour was related to L.H. stimulation received empirical support by Wayner, Greenberg, Fraley and Fischer (1973), in which they demonstrated that L.H. electrical stimulation could serve as,

"an adequate substitute for delivery of
the food pellet under typical conditions
of schedule-induced polydipsia".

Unfortunately this study was based upon one experimental subject, and accordingly the authors recognise the tenuous nature of their findings. Furthermore, it is difficult to compare the schedule-induced polydipsia obtained with this procedure to that of the more usual approach in such a small sample, and without an analysis of the temporal distribution of licking behaviour. However, these findings do implicate the L.H. in the mediation of adjunctive behaviour, and support complementary theories of displacement.

The importance of Wayner's approach lies in the clarification of the anatomical systems involved in adjunctive behaviour. It is not, in itself, an explanation of why adjunctive behaviour develops, rather it is an account of how this behaviour might be mediated by the nervous system of the organism. As such it complements

other approaches to the phenomenon.

(E) Some Temporal Considerations.

Schedule-induced polydipsia has characteristically been described as a post pellet phenomenon, eg. Falk (1972) notes,

> "Adjunctive behaviour occurs typically in the immediate post-reinforcement period. In the polydipsic case, *a burst of drinking ensues immediately after each pellet is consumed* * (Falk, 1961a). This occurs on a variety of interval and ratio schedules (Falk, 1961b, 1966b). Although it is tempting to view this drinking burst as a fluid-intake response to meal termination, adjunctive behaviours other than polydipsia occur in the immediate post-reinforcement period when water is not present".

The post-pellet locus of polydipsia has been invoked as evidence in both Stein's (1964) dry-mouth theory, and in Falk's (1969) suggestion which related polydipsia to the low probability of reinforcement shortly after food delivery. Despite common acceptance as to the immediate post-pellet locus of polydipsia (eg. Stein, 1964; Segal, 1969; Keehn, 1970; Wayner, 1970) a number of studies have noted that it may occur at other later times in the post-pellet interval.

*(*italics mine*).

Keehn and Colotla (1971) examined the relationship between level of polydipsia and the interpellet interval (using F.I. schedules). They summarised their findings as,

> "At shorter FIs drinks occured frequently shortly after reinforcement, and drink durations and frequencies varied directly with internal length. At longer intervals, drinking seldom occurred after reinforcement but was more frequent later in the interval. Late drinks were usually brief".

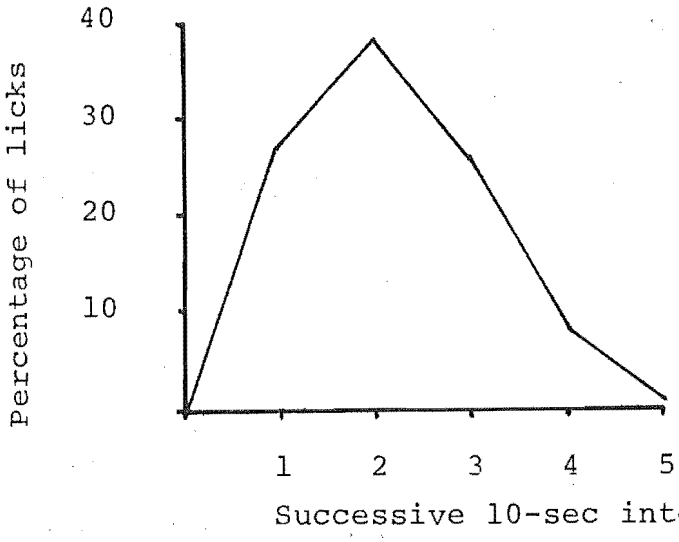
Flory and O'Boyle (1972) presented their subjects with a FI 60 schedule, with an added procedure that prevented drinking over various 15 second portions of the interval following food delivery. They found that this procedure produced only a slight attenuation of polydipsia, compared with the usual procedure, whereby water was continuously available. Gilbert (1974) extended this research, restricting access to the water over various portions of the inter-pellet interval, and concluded,

> "that schedule-induced polydipsia by rats is a post-prandial phenomenon only when post-prandial drinking is possible". [1.]

Schaeffer and Salzberg (1973) analysed the distribution of licking on a FFI 50 schedule as their subject developed polydipsia. At asymptote they found

1. These two experiments are further discussed in Chapter 4.

the licking occurred in the second 10 second interval was attributed to the time required to ingest the pellet and approach the drinking spout in the first 10 second interval.



However, the data were derived from one subject, and no replication using a larger sample appears to have been made.

Killeen (1975), amongst a series of experiments examining several behaviour classes, investigated schedule induced polydipsia in four rats (one of which was subsequently discarded because of idiosycratic behaviour). This study investigated the temporal distribution of polydipsia at asymptote, and the data were applied to a mathematical model of the temporal control of behaviour according to two derived parameters that related to,

> ".....indices of arousal level and inhibitory processes that detract from that level".

The results disconfirmed polydipsia as a post-pellet phenomenon, finding that,

> ".....while there is some post-pellet drinking, the maximum rate of drinking occurs halfway through the interpellet interval".

While this study presents an elegant analysis of the data over a range of interpellet intervals, the results are equivocal on the basis that the subjects had to bar-press to obtain water (on a CRF schedule). As Wayner and Greenberg (1973) noted, bar-pressing itself can be considered as an adjunctive behaviour, which suggests the possibility of some contamination in these results. This methodological factor seems to have been overlooked, as a drinkometer could record the same data.

(F) An Experimental Direction.

In considering schedule-induced polydipsia, it becomes apparent that there have been many attempts to provide an explanatory account for this phenomenon. However, the comments of Hawkins *et al* (1972) remain appo site, for although there ave been several parametric investigations of specific factors, a number of areas of uncertainty remain outstanding,

> "with the primary cause of confusion being the lack of general information about the phenomenon. (Hawkins *et al*, 1972).

As mentioned in the previous section, a sign-ificant area of contradictory evidence relates to the

temporal locus of schedule-induced polydipsia. Clearly any explanation of this phenomenon must remain premature unless the temporal locus of this behaviour is defined.

The research reported in this thesis has been concerned primarily with the temporal distribution of schedule-induced polydipsia. The methodological factors specified were chosen so as to provide a basis for generalisation free of many of the factors shown to influence the phenomenon. By eliminating the bar-press contingency, and selecting an optimum inter-pellet interval it was intended to control for sources of contaminated results, and provide a simple reliable paradigm for other studies.

A further aspect of schedule-induced polydipsia which was investigated, concerned the species-generality of this phenomenon. As was mentioned in section A, polydipsia has been reported over a range of species. However, a number of recent studies have noted a failure to obtain polydipsia in certain species.

The most significant of these negative findings is that of Whalen and Wilkie (1977), who were unable to replicate the results of Shanab and Peterson (1969), who reported polydipsia in the pigeon. Waler and Wilkie used a similar procedure as Shanab and Peterson, but found

> "Frequently, no measureable amount of water was consumed; at most, only a few grams were consumed. This absence of schedule-induced drinking in the pigeon also has been found

recently in other labs (Dale; Fraser)."

They pointed out that Shanab and Peterson's results were based upon a single subject, and that the level of drinking reported was not as excessive as that reported in rats. They concluded that their negative results,

> "adds to the growing list of boundary conditions for schedule-induced phenomenon".

A further failure to obtain schedule-induced polydipsia was reported by Wilson and Spencer (1975), using golden hamsters. They noted that most studies demonstrating polydipsia have used species that show a decrease in water consumption when food deprived. However, hamsters and gerbils do not show a decrease in water consumption under food deprivation (Kutscher, Stillman and Weiss, 1968a, 1968b). Wilson and Spencer related these findings to the desert ecological niche of these latter species, and commented that,

> "more comparative research is needed if the underlying determinants of schedule-induced polydipsia are to be specified."

Prompted by Wilson and Spencer's failure to demonstrate polydipsia in hamsters, Porter, Sozer and Moeschl (1977) further examined the "species limitations" of this phenomenon. Using guinea pigs as subjects they found that two of three subjects developed schedule-induced polydipsia, and that these animals,

> "usually drank immediately following pellet delivery (in those intervals in which

drinking occurred)."

Significantly, only one subject consumed water to a level comparable with rats (subject GP-7 consumed an average of 19.55 mls in the last three polydipsic sessions, whilst the other polydipsic subject GP-6 recorded an average intake of 5.2 mls). These author's, in discussion their results state,

> ".....the results of the present study *clearly demonstrate** that schedule-induced polydipsia can be shown in guinea pigs. The present data extend the generality of schedule-induced polydipsia to a new species and indicate the importance of further studies on the species generality or limitation of schedule-induced polydipsia and other schedule-induced behaviours".

In the light of their results (with only one subject showing polydipsia to a level comparable with rats) their assertion that their results "clearly demonstrate" polydipsia in guinea pigs seem precipitate, especially as they also discuss the findings of Freed, Zec and Mendelson (1977) who,

> "have reported that guinea pigs will display schedule-induced licking of a cold metal tube, but they *failed to find any evidence of schedule-induced polydipsia in guinea pigs** (Porter, Sozer, and Moeschl, 1977).

(* *Italics mine.*)

In the light of this study the only thing that is "clearly demonstrated" is the need for a replication of Porter *et al's* study with a substantial sample size.

A further dimension of species-specificity was examined in a report by Symons and Sprott (1976), who compared two strains of mice; one of which was susceptible to the development of schedule-induced polydipsia, and one of which was not. By pairing these two strains and subjecting the offspring to genetic analysis they found evidence of two alleles being involved - sip^d (dominant susceptible) and sip^b (non-dominant recessive) - and they suggest that there exists genetic variance for this trait. They related these findings to ecological and phylogenetic factors involved in schedule-induced polydipsia.

The likely relationship between schedule-induced polydipsia and phylogenetic/ecological factors suggests that it would be a suitable phenomenon to study using a comparative analysis. By combining the laboratory specifications known to induce polydipsia with information pertaining to the "natural" environment, a synthesis of the approaches of comparative psychology and ethology is possible. This approach allows for an investigation of both the temporal distribution, and the species-generality of this behaviour, and also provides a source of further empirical investigation.

C H A P T E R T H R E E

GENERAL EXPEPIMENTAL RATIONALE.

In the preceeding chapters discussion on schedule-induced polydipsia was concerned with some of it's fundamental variables, with the relationship between polydipsia and other behaviours and with some of the theoretical explanations of this phenomenon. In this discussion it was noted that a number of issues were not empirically resolved; consequently any theoretical account must remain tenuous. In particular, two important issues were highlighted as having significant bearing upon an understanding of this behaviour.

Firstly, although schedule-induced polydipsia has been described as "an immediate post-pellet phenomenon," some studies have challenged this generalisation, and have suggested that the temporal locus of this phenomenon may extend throughout the whole inter-pellet interval. As has been noted, the post-pellet locus has been invoked as evidence against some explanatory accounts of polydipsia.

Secondly, schedule-induced polydipsia has been reported in a number of species, and this species-generality has been considered as important to overall accounts of the phenomenon. However, many of the reports using other species have not been adequately replicated, and doubt

as to the extent of the species-generality of polydipsia exists. Clearly the role of phylogenetic factors must influence any attempt to explain the phenomenon.

The research reported herein concerns these two issues relating to schedule-induced polydipsia. In order that they be studied, an experimental paradigm was devised that permitted an evaluation of both without compromising the unique features of the data obtained from each. Essentially this was achieved by keeping the paradigm simple, by minimising the learning requirements in the experimental situation, and by permitting an adequate sampling of behaviours over time. The paradigm was based upon each of the characteristics of these two research goals, the individual features of these are described separately below.

(A) The Temporal Distribution of Polydipsia

In order that a stable pattern of drinking behaviour be obtained, a fixed-interval schedule was chosen, since this schedule permits the subject to learn the temporal probability of food delivery in a relatively short time. The inter-pellet interval is a significant variable in schedule-induced polydipsia (see Falk 1966b) as intervals of less than 30 and greater than 300 seconds induce insignificant levels of polydipsia in the rat. Thus a 100 second inter-food[1] interval was selected, as it was near

1. The term "inter-food interval" is used here since it applies to those studies using ferrets as well as rats, and is favoured over "inter-reinforcement interval," which term has a specific behaviouristic interpretation that may not be valid in this instance.

the optimal interval, as determined empirically by Falk, and also it would permit a convenient time-base for the analysis of the data.

Since the bar-press response has been suggested as being an adjunctive behaviour itself (Wayner and Greenberg 1973), and also increases the learning complexity of the experimental situation, a response non-contingent procedure was adopted (i.e. a FFI 100 sec schedule of food delivery). This schedule had the advantage of minimising the learning-demands of the experimental situation and provided sufficient time between successive food deliveries for the subjects to engage to some magnitude in the behaviour of interest.

(B) Species Generality Considerations.

The choice of the ferret as a comparison subject with the rat was based upon a number of considerations. A major reason relates to the different ecological niches that these two species occupy. The rat is a typical omnivore, deriving energy from a wide range of food sources, and occupying a broad ecological niche. The ferret is typical of a small carnivore, living on meat protein that it obtains either as live prey, or as carrion (Marshall, 1963, reports that ferrets were observed as preying on diverse species as rabbits, Australian oppossum, rats, mice, birds, frogs, as well as various carrion). As a conseq-uence of their differing ecological niches, rats and ferrets exhibit different patterns of behaviour in the

laboratory setting, and these patterns may determine whether schedule-induced polydipsia (or alternative adjunctive behaviours) occurs, or not. These differences in laboratory behaviour are discussed in more detail in Chapter 5, in which the responses of ferrets to non-contingent food delivery are examined.

Another justification for using the ferret as an experimental subject related to its history as a research subject at the Psychology Department, University of Canterbury. Over the decade they have been kept, suitable handling and husbandry techniques have been developed, such that they have become reliable economical subjects for animal behaviour studies. Accordingly, any research obtained from ferrets would further contribute to the on-going collection of data on this species. Furthermore, their small size and tractable behaviour make them a suitable carnivore to study, as they pose a minimal danger to the experimenter (eg. compared with the larger carnivores). Although they were tractable and tame. they quickly reverted to the appropriate feral behaviour on the rare instances when they escaped the laboratory, and thus their behaviour was presumed to be minimally influenced by their domestic upbringing.

(C) Equivalent Levels of Deprivation.

As has been discussed, the generally adopted level of food deprivation in studies of polydipsia in the rat is

80% free-feeding weight. However, it is not valid to assume that 80% free-feeding weight in the ferret is equivalent to this level in the rat because of biological and ecological differences between these species. Therefore a problem exists as to the determination of a suitable level of food deprivation in the ferret that is likely to produce adjunctive behaviour.

Experience within the animal laboratory had suggested that a suitable level of deprivation in the ferret for extended experimentation could be obtained by reducing the subjects to 90% free-feeding weight and thereafter maintaining this weight by restricting feeding to once every 24 hours. Usually this daily food is given either in the experimental situation, or immediately afterwards. At this level of food deprivation the subjects maintained vigorous eating behaviour without hoarding occurring: hoarding behaviour being related to low levels of food deprivation.

Accordingly, a pilot study was conducted upon two male and two female ferrets, aged 1 year, in which they were subjected to four levels of food deprivation, and a record of their eating behaviour was made. The levels of deprivation used were - 2 hours, 24 hours, 48 hours (all at free-feeding weight) and 24 hours at 90% free-feeding weight. It should be noted that these ferrets were slightly overweight due to over-feeding and lack of activity in the laboratory environment. An additional factor contributing to their being overweight related to the tendency to hoard food in the home cage (necessitating regular searches to remove caches from previous feedings).

Method:

The subjects were tested on the 2, 24 and 48 hour deprivation conditions according to a randomised design, and then reduced to 90% of their original weight and re-tested at the 24 hour deprivation level. The subjects were initially placed in the experimental chamber for 2 successive 15 minute habituation trials (days 1 and 2) - this apparatus was used in all successive ferret studies - (for details see Appendix 4). During the experimental sessions, 30 pieces of meat (weighing 1 - 1.5 grams) were placed in the food receptacle, and the subject introduced to the chamber. The results were obtained by observing the subjects and recording the following data -

(1) latency of eating.

(2) percentage of food pieces consumed during the session.

(3) latency before other behaviours occurred after eating had commenced.

(4) whether hoarding of food occurred.

Results:

These are summarised in Tables 3.1, 3.2, 3.3, and 3.4.

Discussion:

These data indicate that 24 hour deprivation at 90% free-feeding weight was the most suitable deprivation level to adopt for these subjects. Not only did eating occur at a reliable level, but observation of the subjects indicated that intrusive behaviours (such as "scrabbling" at the apparatus door, chewing the food receptable, and hoarding) were occurring to a minimal extent. A further

Table 3.1: Latency of Eating (seconds)

Subjects	2 hours	24 hours	48 hours	24 hours (90% F.F.W.)
M1	37	12	4	5
M2	61	9	2	3
F1	46	32	8	2
F2	17	25	3	1
Means	40.25	19.25	4.25	2.5

Table 3.2: % Food Pieces Consumed in the Session

	2 hours	24 hours	48 hours	24 hours (90% F.F.W.)
M1	13.3	60.0	96.6	100.0
M2	6.6	46.6	93.3	96.6
F1	10.0	76.6	100.0	100.0
F2	20.0	43.3	96.6	100.0
Means	12.5	56.6	96.6	99.1

Table 3.3: Latency of Occurrence of Other Behaviours (secs)

	2 hours	24 hours	48 hours	24 hours (90% F.F.W.)
M1	5	54	176	201
M2	2	18	91	97
F1	37	14	112	165
F2	11	31	194	227
Means	13.75	29.25	143.25	172.50

Table 3.4: Occurrence of Hoarding Behaviour.

	2 hours	24 hours	48 hours	24 hours (90% F.F.W.)
M1	+	+	-	-
M2	-	-	-	-
F1	+	+	+	-
F2	+	-	-	-

advantage of this particular level of deprivation related to the husbandry of this species, since previous experience with ferrets had shown that they could be maintained at this level without any deleterious effects upon their health. Accordingly, this level of deprivation was adopted for the experiments on ferrets.

(D) The General Paradigm and Method of Analysis.

The subjects (laboratory rats and ferrets) were placed in an experimental situation whereby portions of food were delivered on a response non-contingent 100 second schedule of food delivery. The subjects were food deprived (80% free-feeding weight for rats, 90% free-feeding weight and 24 hours deprivation for ferrets) and were maintained at this level by post-experimental supplements of food as necessary.

Water-spouts were available in the experimental situation, and any contact with these was recorded by a drinkometer onto an event recorder. Provision was made for observation of the subjects in the experimental apparatus.

In order that an adequate data sample be obtained, the subjects received 100 food portions in each daily experimental session, making a session length of 166 minutes per subject.

Learning requirements within the experimental situation were minimised by adopting a response non-contingent schedule of food delivery, by using light and

auditory signals when the food was delivered, and by allowing the subjects several sessions to adapt to the experimental environment before test-sessions were conducted.

The method of analysis employed to determine the temporal distribution of schedule-induced polydipsia was based upon a division of the 100 second inter-food interval into 20 successive units of 5 seconds duration. Due to technical short comings, it was not possible to ascertain the actual number of licks in each 5 second unit ('bin'), so the data was based upon whether licking was present or not. Since there were 20 successive bins, the distribution obtained by this method was considered to be reasonably sensitive, especially when summated over 100 food deliveries. The final data obtained by this method took the form of the empirical probability of licking occurring in each bin thus generating a temporal distribution of the licking behaviour. Concommitantly with the determination of this distribution, the amount of water consumed and the total number of licks in each session were recorded as additional data.

This paradigm was used in all the studies conducted on rats and ferrets, although those studies reported in Chapter 6 used a modified form of analysis (see Chapter 6).

C H A P T E R F O U R

THE TEMPORAL LOCUS OF SCHEDULE-INDUCED POLYDIPSIA.

(A) Introduction.

(B) Experiment 1: A Pilot Study.

- Subject
- Apparatus
- Procedure
- Results
- Discussion
- General Discussion: The Importance of the Drinking vs. Licking Topographies.

(C) Experiment 2: A Comparison of the Drinking and Licking Topographies.

- Subjects
- Apparatus
- Procedure
- Results
- Discussion
- General Discussion.

(D) Experiment 3: A Further Comparison of the Drinking and Licking Topographies.

- Subjects
- Apparatus
- Procedure
- Results
- Discussion
- General Discussion.

(E) An Overview.

CHAPTER FOUR

THE TEMPORAL LOCUS OF SCHEDULE-INDUCED POLYDIPSIA.

(A) Introduction:

As has been previously discussed, Falk's generalisation regarding the temporal locus of schedule-induced polydipsia as being "an immediate post-pellet phenomenon" has been challenged by other reseachers. Of note are studies by Flory and O'Boyle (1973), and Gilbert (1974), this latter author described schedule-induced polydipsia as occurring "whenever drinking was possible", and noted that "schedule-induced polydipsia by rats is a post-prandial phenomenon only when post-prandial drinking is possible". Although these two studies have examined aspects of the temporal locus of polydipsia, and have challenged the accepted view of this phenomenon, they are open to criticism on methodological grounds.

Flory and O'Boyle used a procedure whereby food was available on a FI 60-sec schedule, and water was obtained via a second response lever operating on a FR 1 schedule This second lever was retractable, and consequently water was made unavailable over various quarters of the inter-pellet interval. Their results noted a slight attenuation of drinking under those conditions where the water was partially unavailable, and they concluded that,

"the introduction of the 15-sec periods

> of water unavailability generally resulted in the shifting of drinking to the time periods when the water lever was accessible".

In view of the procedure they used, this conclusion is hardly surprising, since drinking was impossible in the absence of the lever.

Gilbert adopted a similar procedure, but removed the bar-press contingency for water, and substituted a retractable drinking tube for the water lever. He used both contingent schedules (FI 60-sec) and non-contingent schedules (FFI 60-sec, FFI 210-sec) of food delivery and confirmed similar findings to those of Flory and O'Boyle. The importance of these results notwithstanding, both these studies have serious methodological shortcomings. Firstly, the use of the bar-press contingency (for either food or water) is a possible source of confounded results, since Wayner and Greenberg (1973) had demonstrated that the bar-press response itself may be an adjunctive behaviour. Secondly, the use of retractable levers and drinking tubes may introduce the problem of these items becoming discriminative stimuli, since the probability of these items being available is variable, and it is possible that they may acquire attentional (discriminative) properties related to their availability. Thirdly, in the absence of an opportunity to engage in polydipsia (due to the drinking tube not being present) alternative adjunctive behaviours may occur, which are not measured, and which may cease as soon as the drinking tube reappears permitting drinking.

An alternative method is that used by Schaeffer and Salzburg (1973) who used a FFI 50-sec schedule of food delivery, and recorded the sum of licks occurring in each of 5 successive 'bins' of 10 seconds duration. Since the drinking tube remained constantly available, and food delivery was response non-contingent, the overall procedure was markedly simpler and free of the difficulties associated with the use of retractable levers and drinking tubes. Unfortunately the results of Schaeffer and Salzburg's study are based upon a single subject, but they noted that the drinking became "concentrated predominantly as a post pellet event within the first FFI sesson". A similar procedure was adopted by King and Schaeffer (1973) in that they divided the interpellet interval of a FI 60-sec schedule into four 15-sec periods and counted the number of licks in each period. However, they relied upon the bar-press response to provide food, and therefore the aforementioned criticisms of this technique are relevant. The results of this study confirmed the findings of Schaeffer and Salzburg, namely , "licking did not occur with equal probability in all periods of the interpellet interval but tended to occur immediately after pellet delivery from the early stages of SIP development".

Since the general experimental paradigm described in Chapter Three adopted a response non-contingent food delivery schedule (FFI 100-sec), and the drinking tube remained in a place throughout the experiment, the results obtained are comparable with those of Schaeffer and

Salzburg. The first experiment conducted was a pilot study to evaluate the methodological paradigm mentioned above, and during the course of this experiment a fortuitous discovery that 'the subject would lick at a tube which did not permit drinking to occur' provided an additional methodological dimension, the importance of which is pursued in the discussion section of this study.

(B) Experiment 1: Pilot Study.

Subject:

One experimentally naive female hooded rat, aged 180 days and weighing 184 grams served. The subject was reduced to 80% free-feeding weight for the duration of the experiment. Daily feeding comprised 100 pieces of wheat in the experimental setting (approximately 5 grams) with a post-experimental supplement of laboratory animal food to maintain the desired weight: details of the food and laboratory housing procedures are given in Appendix 4. Water was continuously available in the home cage.

Apparatus:

The experimental apparatus used was Rat Chamber 1 (see Appendix 3 for details). The subject was fed 1 grain of wheat every 100 seconds from a Davis Universal Feeder. A drinking tube was continuously available in the experimental chamber, and was connected to a graduated pipette and water reservoir. Two drinking tubes were used, one having an aperture of 6.0mm^2 (and from which drinking was possible - the *drinking tube*) the other had an

aperture of 0.8mm^2 (and from which drinking was not possible - the *licking tube*).

Procedure:

The daily home cage water consumption was recorded for 7 days before the introduction of the 80% free-feeding weight condition, and for 7 days afterwards (to obtain baseline data). The subject was then introduced to the experimental apparatus for a 30 minute period on 2 successive days and given 100 pieces of wheat simultaneously in the food receptacle, so as to familiarise the subject with both the apparatus and the food source.

There followed 14 daily sessions during which 100 pieces of wheat were individually delivered on a FFI 100-sec schedule. Schedule-induced polydipsia was observed to develop to a stable level (i.e. to asymptote) over the first 8 sessions. On sessions 9, 11, 13 and 14 the licking tube was substituted for the drinking tube, the drinking tube being reinstated on sessions 10 and 12. During these experimental sessions the daily level of home-cage drinking was recorded, as was water consumption and the number of licks in the experimental situation. The temporal distribution of schedule-induced polydipsia was recorded on session 12, while the distribution for the licking tube was obtained on session 14.

Results:

(a) Water Consumption: The data pertaining to home cage consumption under normal bodyweight and at 80% free-feeding weight are given in tables 4.1 and 4.2, and indicate a

Table 4.1:

Daily Homecage Water Intake: 100% Free Feeding Weight.

Day	1	2	3	4	5	6	7
Intake (ml's)	13.2	9.8	11.6	10.7	15.9	14.2	13.8

Mean: 12.7 ml's

Table 4.2:

Daily Homecage Water Intake: 80% Free Feeding Weight.

Day	1	2	3	4	5	6	7
Intake (ml's)	7.4	7.0	9.9	8.4	10.3	11.1	10.6

Mean: 9.25 ml's

mean daily consumption of 12.7 ml's and 9.25 ml's respectively. Water consumption under the experimental conditions is summarised in columns 4 (*Experimental Conditions: Water Intake*), 5 (*Home Cage: Water Intake*) and 6 (*Total Daily Water Intake*) of table 4.3 (*Summary of Experimental Conditions*).
The water intake under the experimental conditions is given in Figure 4.1, showing amount of water consumed (ml's) versus daily sessions. The data on water consumption indicate a decrease in daily water intake when the 80% free-feeding weight condition was imposed (this decrease being in the order of 25%) and an increase in water consumption in the experimental conditions when schedule-induced polydipsia developed (this increase being in the order of 260% at asymptote). During those trials when the drinking tube was substituted for the licking tube the daily water consumption fell back to the normal 80% free-feeding weight levels.

(b) Number of Licks: The total number of licks as recorded by the drinkometer, are summarised in column 3 of Table 4.3 (*Summary of Experimental Conditions*), and also are presented in Figure 4.2 showing total licks versus sessions. These data indicate the number of licks reached asymptote about session 6, when a stable pattern of about 5800 $\pm$ 400 licks was recorded per session. A decrease in licking occurred when the licking tube was first introduced in session 9, but thereafter attained comparable levels as the drinking tube when further licking tube sessions were conducted.

(c) The Temporal Distribution of Drinking and Licking:
The temporal distributions were derived from data obtained from session 12 (drinking tube condition) and session 14

Table 4.3: Summary of Experimental Conditions

D: Drinking Tube.
L: Licking Tube.

Session	Tube Conditions	Number of Licks	Experimental Condition Water Intake (ml's)	Home Cage Water Intake (ml's)	Total Daily Water Intake (ml's)
1	D	1984	7.8	3.1	10.9
2	D	2987	18.4	0.9	19.3
3	D	4861	21.7	2.1	23.8
4	D	5409	28.3	0.5	28.8
5	D	6309	29.9	1.7	31.6
6	D	5796	27.4	0.4	27.8
7	D	6066	33.0	1.3	34.3
8	D	5838	31.6	1.6	33.2
9	L	4893	0.0	7.8	7.8
10	D	6109	34.8	0.6	35.4
11	L	6791	0.0	6.4	6.4
12	D	5994	32.4	3.1	35.5
13	L	6268	0.0	8.6	8.6
14	L	6847	0.0	9.8	9.8

Figure 4:1 Water intake per daily session.

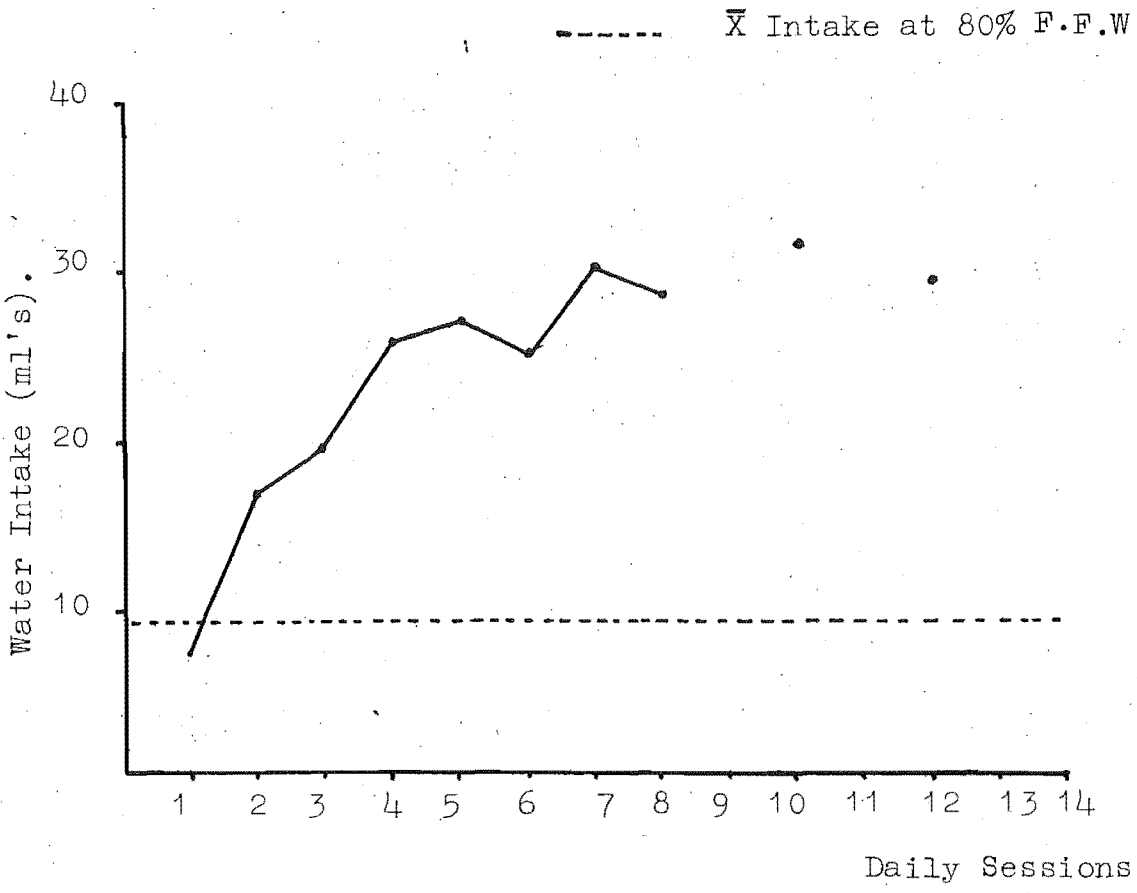
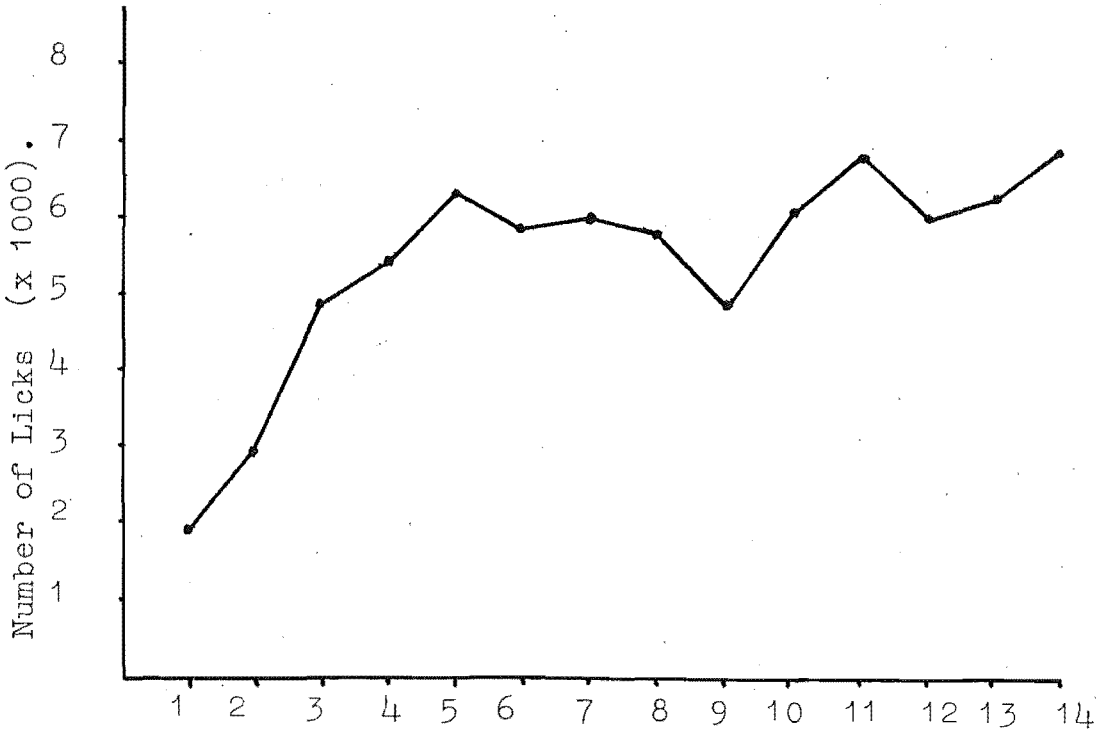


Figure 4:2 Total licks per daily session.



(licking tube condition). The raw data was in the form of event-record charts indicating the points where food delivery occurred on one channel, with drinkometer contacts on the other channel. Taking the commencement of food delivery as the starting point of a cycle, the 100 second interval was divided into 20 successive 5 second units (bins), the last of these bins being followed by the next cycle. There were 100 cycles of food delivery in each daily session.

Each successive bin was scored according to whether it contained a drinkometer record or not, and a distribution for each cycle was determined on the basis of this information. The distributions obtained by this method were of a binary nature, since scoring was based upon the presence or absence of drinkometer contacts in each bin, and thus no information on the mangitude of contacts was possible (as the record in each bin may have been derived from one or more licks).

Having ascertained the distributions of drinkometer contacts for each cycle, a total distribution of contacts was obtainable for the daily session by summing each successive bin across all cycles. The ensuing distribution took the form of 20 successive figures (the maximum value of which could never exceed 100, since there were only 100 cycles per daily session). These data could conveniently be expressed as a probability of drinkometer contact for each bin, i.e. as a probability of drinking or licking over successive portions of the inter-food interval.

The distribution of drinkometer contacts for sessions 12 and 14 are presented in Tables 4.4 and 4.5, and also on Figures 4.3 and 4.4. These data are further considered by breaking the total distribution of drinkometer contacts into 'within session' form to ascertain whether there were any changes in the distribution and magnitude of drinkometer contacts over the session length (i.e. to investigate whether a "fatigue" effect was occurring). This breakdown was achieved by summarising blocks of 20 cycles of food delivery, then devising a generalised measure of drinkometer contact. The generalised measure was based upon the summation of all drinkometer contacts in each 20 cycle block, and dividing this figure by a factor of 4 to convert it into a percentage measure (there being 20 cycles x 20 bins making a total of 400 possible drinkometer contacts, assuming the subjects continuously licked or drank to the exclusion of all other behaviours). These data are presented in Tables 4.6 (drinking tube) and 4.7 (licking tube), and are compared in Figure 4.5.

Discussion:

(a) Water Consumption: The decline in mean daily water intake from 12.7 ml's to 9.25 ml's when the subject was deprived to 80% free-feeding weight is an accordance with the expected results, where a reduction of the order of 25-40% is commonly reported, (eg. Kutscher, 1969). Furthermore, the rapid increase in intake when schedule-induced polydipsia develops, with a concommitant decrease in home-cage post-experimental intake, follows the pattern

Table 4.4:

The Temporal Distribution of drinkometer contacts: Drinking Tube

Successive bins:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Inter-food Interval (secs):	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
Probability of drinkometer contact:	.00	.00	.12	.19	.28	.27	.32	.27	.26	.23	.16	.13	.13	.11	.07	.06	.04	.03	.03	.04

Table 4.5:

The Temporal Distribution of drinkometer contacts: Licking Tube

Successive bins:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Inter-food Interval (secs):	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
Probability of drinkometer contact:	.04	.00	.29	.56	.63	.50	.53	.53	.43	.49	.41	.45	.41	.43	.37	.38	.38	.38	.27	.38

Figure 4:3 Temporal distribution of drinkometer contacts. (drinking tube).

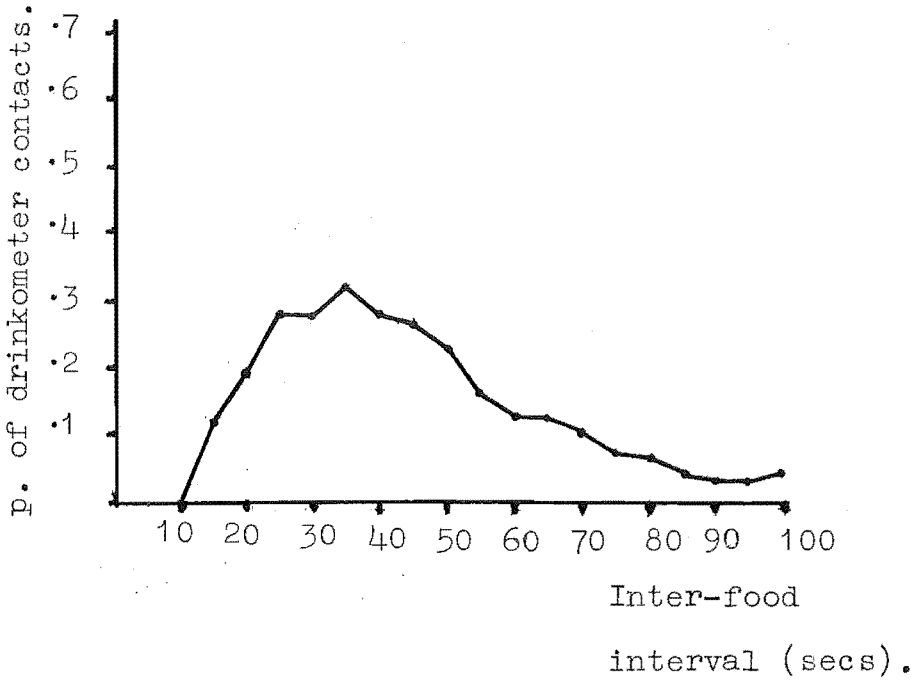


Figure 4:4 Temporal distribution of drinkometer contacts. (licking tube).

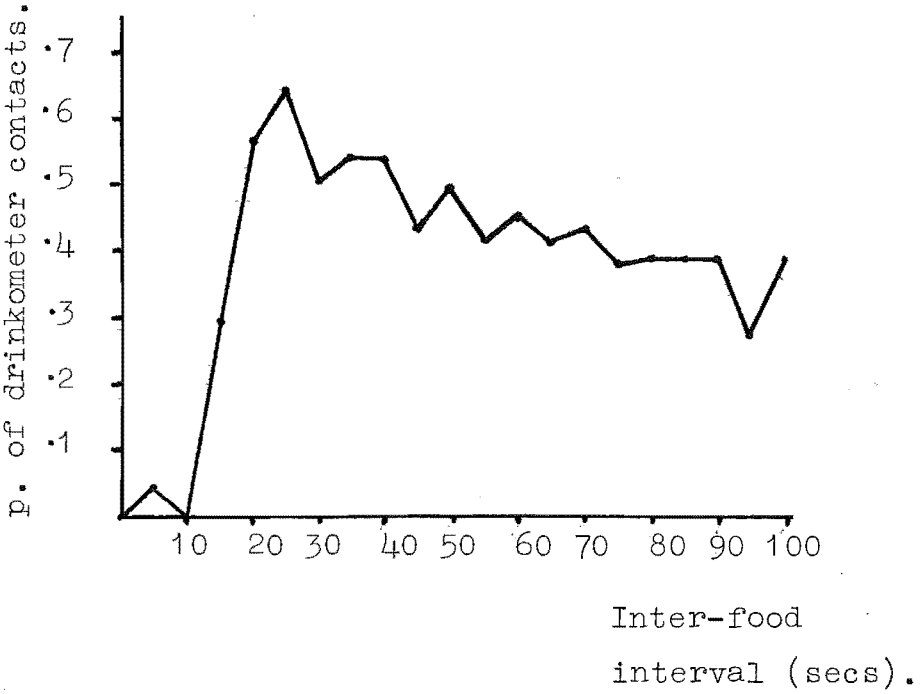


Table 4.6 (Drinking Tube)

Percentage of Drinkometer Contacts per 20 Cycles of Food Delivery.

Cycle of Food Delivery	1 - 20	21 - 40	41 - 60	61 - 80	81 - 100
% Drinkometer Contacts	13.5	10.5	16.75	13.5	13.75

Mean = 13.6%

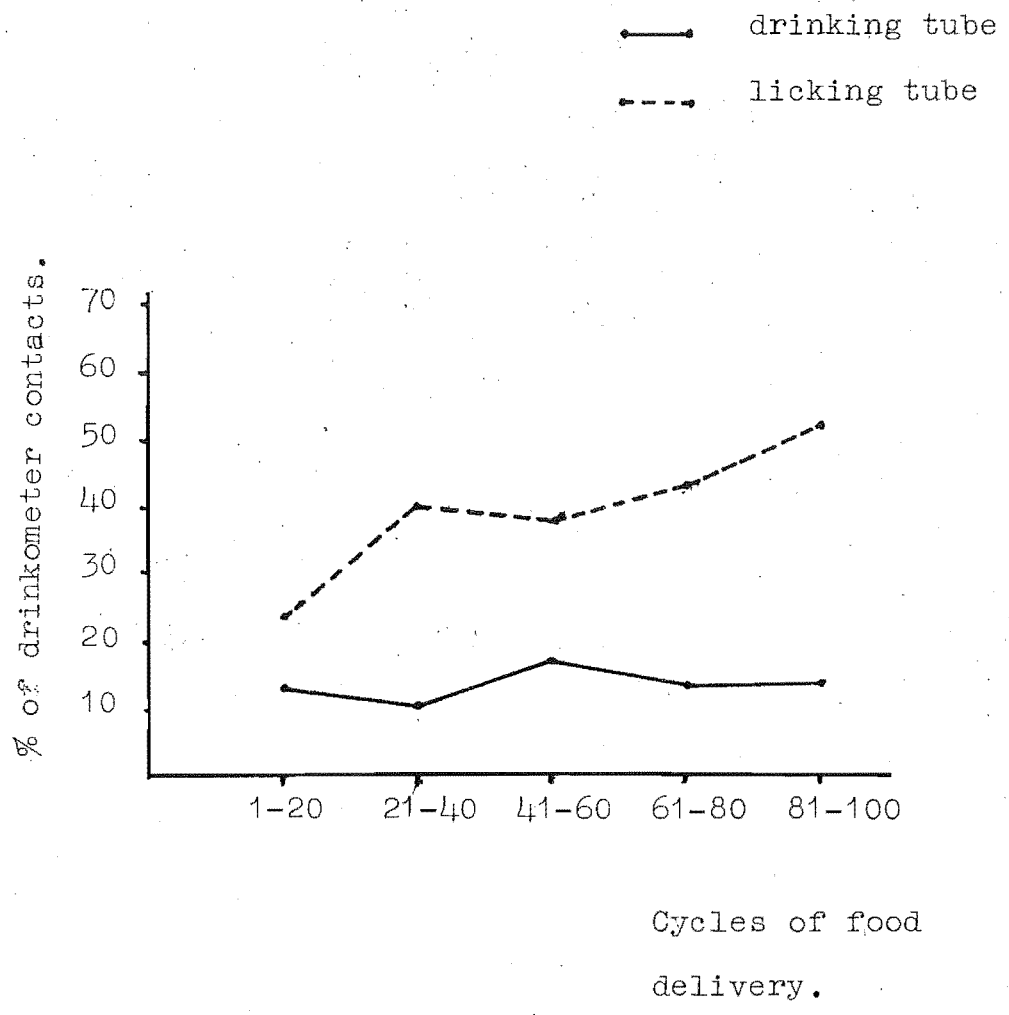
Table 4.7 (Licking Tube)

Percentage of Drinkometer Contacts per 20 Cycles of Food Delivery.

Cycle of Food Delivery	1 - 20	21 - 40	41 - 60	61 - 80	81 - 100
% Drinometer Contacts	23.5	40.25	38.25	43.25	52.25

Mean = 39.5%

Figure 4:5 Percentage of drinkometer contacts per block of 20 food-delivery cycles.



reported by Falk. As Figure 4.1 indicates, the level of drinking rapidly exceeded the recorded daily home-cage level of drinking, and reached asymptote by session 7. Of particular interest is the daily home-cage consumption on those days when the licking tube condition was operating; the levels recorded on these occasions being within the normal range of the baseline data (i.e. at 80% free-feeding weight).

(b) Number of Licks: The finding that licking occurred at a comparable level on a tube that did not permit drinking was both a fortuitous, and totally unexpected discovery. The drinking tube was cleaned daily, the reservoir and tube being disassembled at the end of each session, and re-assembled and refilled with fresh water at the beginning of each new session. At the end of session 8 the drinking tube was inadvertantly placed in a box containing another tube, and this was alternate tube was substituted in its place on session 9. It was not until the water intake was measured at the end of the session that the peculiarity of the results was noted: although a high level of licking had been recorded, no water had been consumed. An examination of the drinking tube revealed both the substitution of the tubes and the reason for the absence of water consumption. The licking tube had a very small aperture ($0.8mm^2$) which permitted a very slight water flow if the wire in the centre of the tube was removed. This wire was inserted in the drinking tube to allow air-bubbles to move around a bend in the tube, and thereby equilibrate the air pressure in the water-reservoir. In the case of this particular tube, the wire had lodged

in the aperture of the tube, and prevented water flowing through the aperture. Thus the licking tube was similar to the drinking tube in all respects except for the important difference of not allowing the subject to obtain water.

The finding that the subject would lick without obtaining water was unexplained, and will be considered in detail in the General Discussion section that follows. However, it is important to note that after the first session with the licking tube, levels of licking with this condition exceeded those for the drinking tube, and suggested the existence of a strong phenomenon. The shape of Figure 4.2 is similar in general shape to Figure 4.1, indicating that licking reached asymptote about sessions 6 and 7 in a similar fashion to water consumption.

(c) The Temporal Distribution of Drinking and Licking:

The data from Tables 4.4 and 4.5, and from Figures 4.3 indicate that the temporal locus of schedule-induced drinking and licking cannot be exclusively described as an immediate post-pellet phenomenon in the case of this subject. Drinkometer contacts were recorded up to the period immediately before the next food delivery (albeit at a low level of probability in the drinking tube condition). If the data from Tables 4.4 and 4.5 are cumulatively summed, they provide data showing a mid-point between bins 7 and 8 for the drinking tube (i.e. between the 35th and 40th seconds of the inter-food interval), while in the case of the licking tube the mid-point is found between bins 9 and 10 (i.e. between the 45th and 50th seconds of the inter-food interval). The only point

where the probability of drinkometer contact falls to zero is that point immediately after food delivery, when the subject is occupied with eating (i.e. within the first 10 seconds of the inter-food interval).

There are a number of differences between the distributions of drinkometer contacts under each condition:

(i) The distribution obtained with the drinking tube is of a lower magnitude compared with that of the licking tube.

(ii) There is a higher probability of drinkometer contacts over the latter half of the inter-food interval with the licking tube.

(iii) The shape of the distribution for the drinking tube describes a near normal curve, whilst that of the licking tube is positively skewed.

A further difference is apparent when Tables 4.6 and 4.7, and Figure 4.5 are considered, showing the within session levels of drinkometer contacts. These reveal that the percentage of drinkometer contacts per 20 cycle block remains relatively stable and at a low level in the drinking tube condition (a mean of 13.6%) while those of the licking tube are at a higher level (a mean of 39.5%) and show an increase across the session (the level in the last 20 cycle block being over 100% more than in the first block).

Consideration of the temporal distributions (and the within session differences) between the two tubes must be limited, since the data is based upon a single subject (and a single session under each condition) and thereby render the data as being attributable to idiosyncracy.

Despite these difficulties, the results indicate the suitability of the general experimental paradigm in producing a stable level of schedule-induced polydipsia.

General Discussion:

The Importance of the Drinking vs Licking Topographies:

The discovery that high levels of licking occurred without water being consumed was unexpected. In criticising the adventitious reinforcement explanation of schedule-induced polydipsia, Stein (1964) had observed that emptying the water bottles of polydipsic rats brought about a complete cessation of licking in a short time and from this observation he concluded that thirst was the primary inducing factor for the excessive drinking. Although this conclusion has been challenged (most notably by Segal and Oden, 1965) there has been general acceptance of the empirical findings regarding emptying of the water bottles. An exception to this finding has been an experiment by Cook and Singer (1976), who noted that emptying the drinking tube produced "a decrease but not complete cessation in licking". In this study they observed that two subjects continued to lick at "approximately 1500 licks per 30 minute session even after eight days with no water present in the tube". They interpreted these results in terms of the general activation of the lateral hypothalamus due to the effects of food deprivation, since they had observed simultaneous increases in other behaviours (eg. bar-pressing, locomotion, grooming, floor gnawing) with the emptying of the water bottles, and they made the added suggestion that those subjects who

continued licking when the water tubes were empty may have been responding to the rewarding effects of the drinkometer current. This latter suggestion bears reference to the finding that rats will lick persistently at a metal spout that is connected to a drinkometer in response to the small electrical current that activates this device (Slangen and Weijnen, 1972; Weijnen, 1972).

In the pilot study, the level of licking obtained using the licking tube was greater than the level recorded from the drinking tube, and is comparatively in excess of the levels reported by Cook and Singer. The magnitudes of licking obtained using these two different tubes suggest a number of possible explanations:

(i) The results are based upon one subject, and therefore might be due to idiosyncratic behaviour in this animal.

(ii) The subject might have been responding to rewarding stimulation effects of the drinkometer current which sustained a high level of licking in the absence of the opportunity to drink.

(iii) The subject may have obtained some rewarding effects from licking at the relatively cool water-spout in the absence of liquid intake (i.e. schedule-induced tongue-cooling as described by Mendelson and Chillag, 1970). This is possible as the water tube and reservoir were filled before each session with fresh tap water at a lower ambient temperature compared with the experimental apparatus, and thereby provided a heat-sink that would keep the tube cool.

(iv) In the absence of a drinking response, an alternative (but related) response topography might be induced, in this

case licking behaviour might be an alterative to drinking behaviour. The possibility of two topographies being induced has been suggested by Segal (1973), personal communication). She has observed that some individual rats licked but removed very little water from the bottle, whilst others removed a greater amount for fewer licks (i.e. this implies that some rats learn to lick at the tube ((and consume some water as a consequence of this behaviour)) while other rats learn to drink with minimal licking behaviour).

(v) The subject, having learned of the spatial location of the drinking tube, may continue to direct adjunctive responses to this location, and in the absence of drinking tube may continue to emit related responses to the alternate tube (i.e. licking in approximation to drinking behaviour).

(C) Experiment 2: A Comparison of the Drinking and Licking Topographies.

Since the pilot study did not examine these potential explanations for the high level of responding on the licking tube, the experiment was repeated with more subjects to further investigate the temporal distributions of responding on the respective tubes, and to confirm that the responding to the licking tube was not an isolated incidence.

Subjects:

2 male and 1 female experimentally naive hooded rats,

aged 180 days were used. The subjects individually weighed 278 grams (M1), 341 grams (M2), and 263 grams (F1). They were individually caged for 2 weeks prior to being food deprived to 80% free-feeding weight. Housing and feeding were similar to the pilot study.

Apparatus:

Due to technical limitations in Rat Chamber 1, an enlarged experimental chamber was constructed to improve viewing of the subjects, to provide more adequate ventilation, and to permit drainage of the copious urine produced during polydipsic sessions: for details of this apparatus see Rat Chamber 2 in Appendix 3. In order that the size and quantity of food be standardized, the use of wheat grains was discontinued, and 40 mg *Animal Food Pellets* were substituded: for details of these see Appendix 4. Food was delivered in the same manner as in the pilot study. Two identical water tubes and reservoirs were used in conjunction with the respective drinking and licking tubes. The drinking tube was *always* sited on the right-hand side wall (position A), whilst the licking tube was *always* sited on the rear wall (position B); these two tubes were spatially separated to a distance of 13.5 cms, in order that they might be discriminated between their respective properties.

Procedure:

Individual daily home-cage water intake was recorded for 6 days prior to the introduction of food deprivation to 80% free-feeding weight. At this level of deprivation

individual home-cage daily water intake was again recorded for 6 days to provide baseline data. On the last 2 days of this condition each subject was introduced to the experimental chamber for a 30 minute period, during which time 30 food pellets were simultaneously available in the food receptacle (to habituate the subjects to the experimental situation and familarise them with the nature and location of the food). During these habituation sessions white noise was present.

Thereafter the subjects received 100 food pellets ona FFI 100-sec schedule for 4 successive days with the drinking tube only present, during which time schedule-induced drinking was observed to develop. On successive days the subjects received the licking tube only on odd numbered days, and the drinking tube only on even numbered days, until day 12 when stable levels of responding were well established. Days 13 to 18 were data recording sessions, during which occasions the temporal distributions of responding were obtained for the licking tube (on days 13, 15 and 17), and for the drinking tube (days 14, 16 and 18). Days 19 and 20 were control sessions, during which times the drinkometers were disconnected, in order that rewarding drinkometer effects might be evaluated. This control was achieved by recording the amount of water drunk on day 19 (drinking tube only), and observing the subjects to see whether they were licking on day 20 (licking tube only). During all experimental sessions daily home-cage water intake was monitored.

Results:

(a) Water Intake: The individual daily water intakes for 100% and 80% free-feeding weight are given in Table 4.8 with means, and indicate the expected decrease of 30-40% when food deprivation is imposed. The daily water intake under the experimental conditions is given in Tables 4.9, and comprises home-cage experimental session, and total - intake data for each animal. This data is also presented in Figures 4.6 a - c, along with the 80% free-feeding weight mean home-cage level. The daily experimental session intake indicates a consistent increase to asymptote about the tenth session, where a level of polydipsia of the order of 100 - 200% increase over the mean daily level was recorded. Home-cage intake levels were depressed on those days following sessions with the drinking tube, indicating a marked delay in the recovery of normal intake levels.

(b) Number of Licks: The number of licks recorded in each experimental session are summarised in Table 4.10, and are also presented in Figures 4.7 a - c. These indicate considerable individual differences between subjects; F1 recorded very few contact with the drinking tube, while M2 recorded contacts in excess of 10,000 with both tubes. The pattern exhibited by M2 (magnitude of contacts aside) is similar to the pilot study subject, whilst subjects M1 and F1 demonstrate dimished licking on the licking tube. Despite these differing patterns all subjects exhibited schedule induced polydipsia; as is shown by the water intake data.

(c) Control Sessions: The water intake on session 19 indicates that all subjects remained polydipsic although

Table 4.8: Daily Pre-Experimental Water Intake (ml's)

Subject.	100% Free-Feeding Weight						Mean	80% Free-Feeding Weight						Mean
M1	9.0	12.5	22.0	24.0	18.5	18.0	17.33	11.4	13.7	12.9	10.1	14.8	14.3	12.86
M2	21.5	5.5	36.0	19.0	18.0	21.0	20.16	16.7	11.5	17.6	14.9	15.2	12.9	14.8
F1	12.0	14.5	8.0	18.0	19.0	19.0	15.08	6.6	8.1	5.3	9.8	12.3	9.8	8.65

Table 4.9: Daily Experimental Session Water Intake:

		M1			M2			F1		
Session	Condition	Exp.	H/C	Total	Exp.	H/C	Total	Exp.	H/C	Total
1	D	6.9	4.1	11.2	2.9	8.7	11.6	5.8	4.4	10.2
2	D	11.6	5.7	17.1	6.3	7.4	13.7	9.4	1.9	11.3
3	D	18.7	0.9	19.6	9.8	4.9	14.7	10.9	0.4	11.3
4	D	22.6	1.3	23.9	12.8	2.6	15.4	16.3	3.1	19.4
5	L	-	5.1	5.1	-	8.3	8.3	-	6.9	6.9
6	D	19.4	0.6	20.0	15.2	1.9	17.1	18.9	0.0	18.9
7	L	-	7.3	7.3	-	4.8	4.8	-	4.0	4.0
8	D	32.3	0.3	32.6	19.7	0.0	19.7	20.4	0.3	20.7
9	L	-	6.2	6.2	-	5.9	5.9	-	1.4	1.4
10	D	34.7	0.0	34.7	30.5	2.8	33.3	23.8	0.5	24.3
11	L	-	7.0	7.0	-	4.4	4.4	-	2.7	2.7
12	D	40.9	0.0	40.9	33.3	3.1	36.4	26.0	0.0	26.0
13	L	-	2.7	2.7	-	6.4	6.4	-	4.5	4.5
14	D	42.8	0.0	42.8	41.3	0.1	43.4	27.4	0.3	27.7
15	L	-	1.6	1.6	-	6.8	6.8	-	3.8	3.8
16	D	42.0	0.6	42.6	35.1	2.9	38.0	25.7	0.6	26.3
17	L	-	1.8	1.8	-	0.3	0.3	-	1.4	1.4
18	D	31.2	3.4	34.6	44.3	0.0	44.3	28.1	0.0	28.1
19	D	36.5	2.9	39.4	39.8	0.9	40.7	26.9	0.0	26.9
20	L	-	4.6	4.6	-	5.1	5.1	-	3.5	3.5

D = Drinking Tube

L = Licking Tube

Figure 4:6 (a) Subject M1. Water intake per daily session.

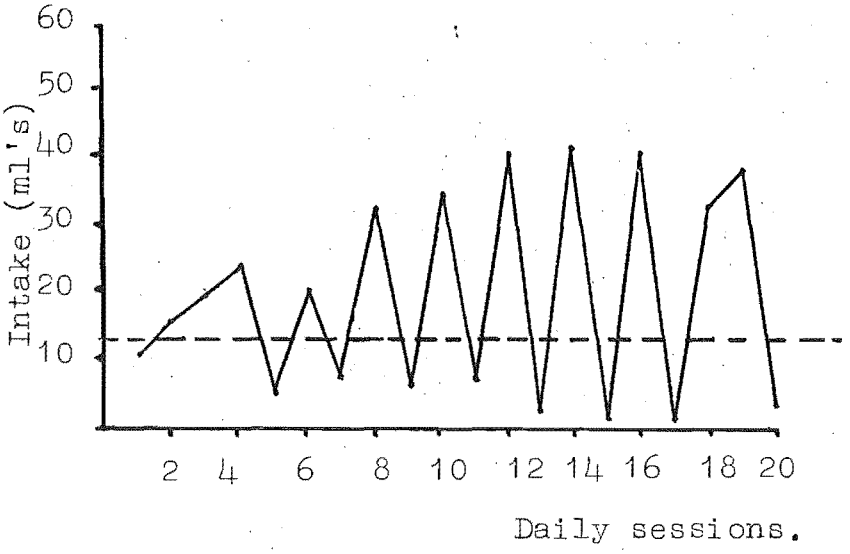


Figure 4:6 (b) Subject M2.

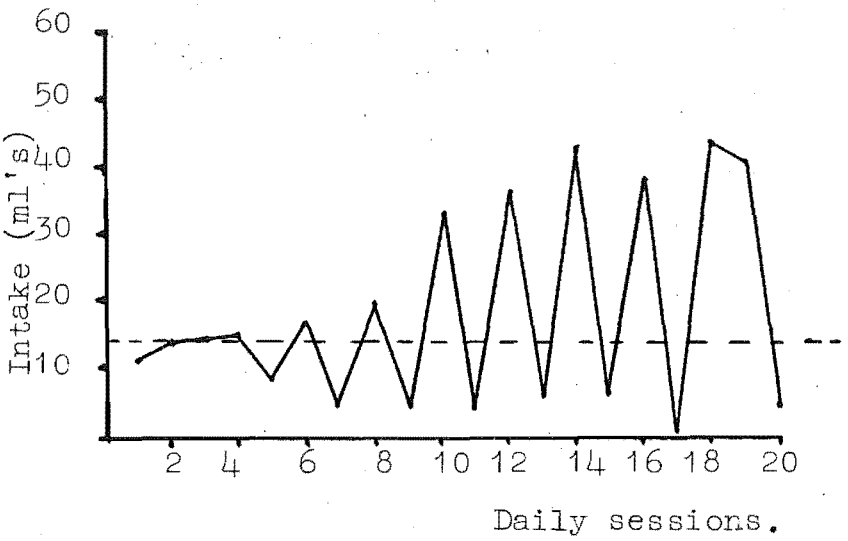


Figure 4:6 (c) Subject F1.

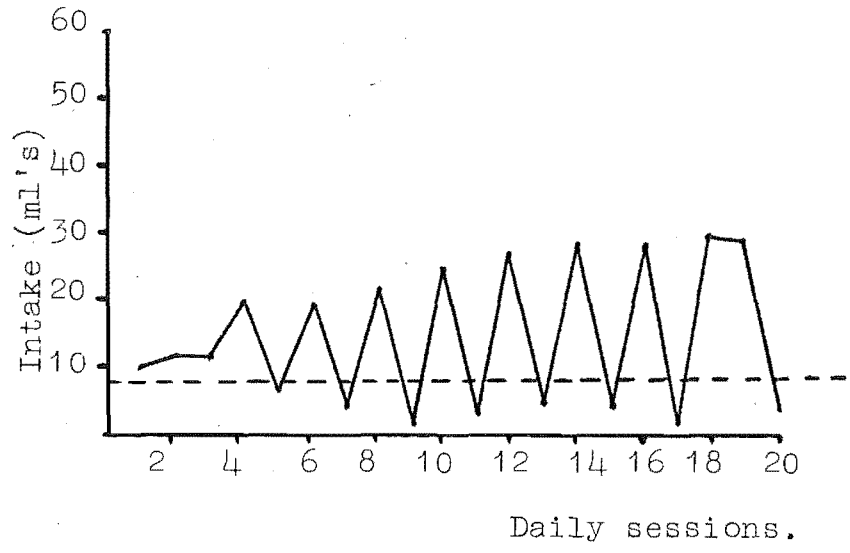


Table 4.10: Number of Licks per Experimental Session.

Session	Condition	M1	M2	F1
1	D	984	1386	1849
2	D	1436	1596	1994
3	D	2814	2104	2017
4	D	2998	2349	2333
5	L	1381	2243	81
6	D	3294	3989	3097
7	L	1409	6309	197
8	D	5803	7964	3271
9	L	1884	9107	429
10	D	5617	9644	4469
11	L	2084	10076	275
12	D	6297	11103	5271
13	L	1423	11334	445
14	D	6464	11866	6994
15	L	2803	4423+	340
16	D	5896	9965	5354
17	L	2373	15825	211
18	D	3536	11041	5401
19	D	-	-	-
20	L	-	-	-

+ Subject was not well.

Figure 4:7 (a) Number of licks per session Subject M1.

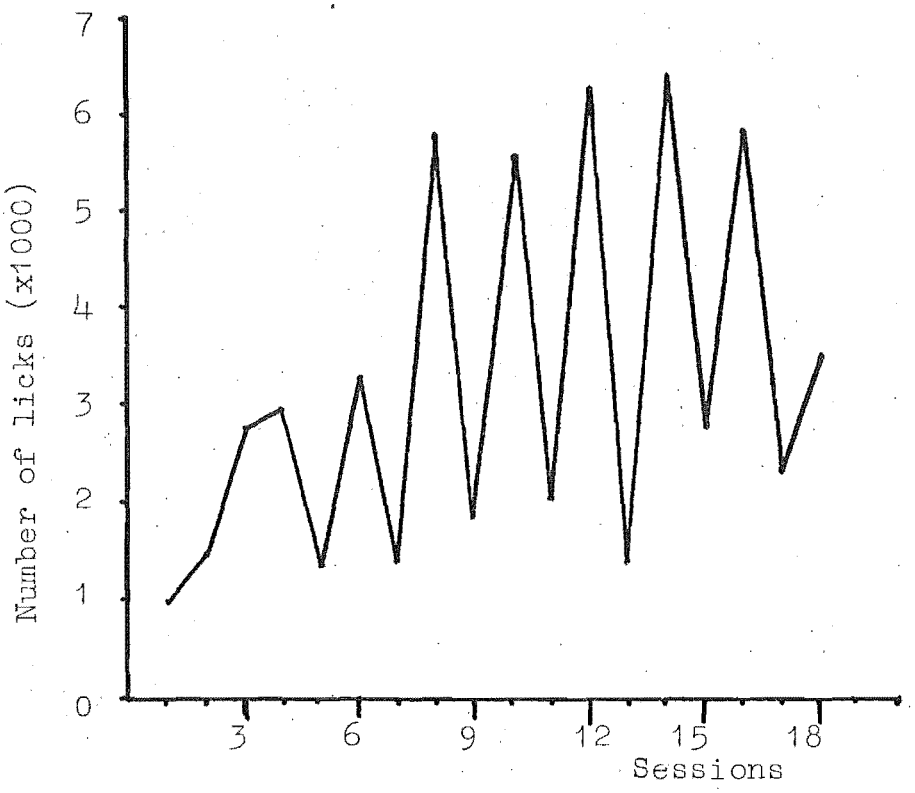


Figure 4:7 (c) Number of licks per session Subject F1.

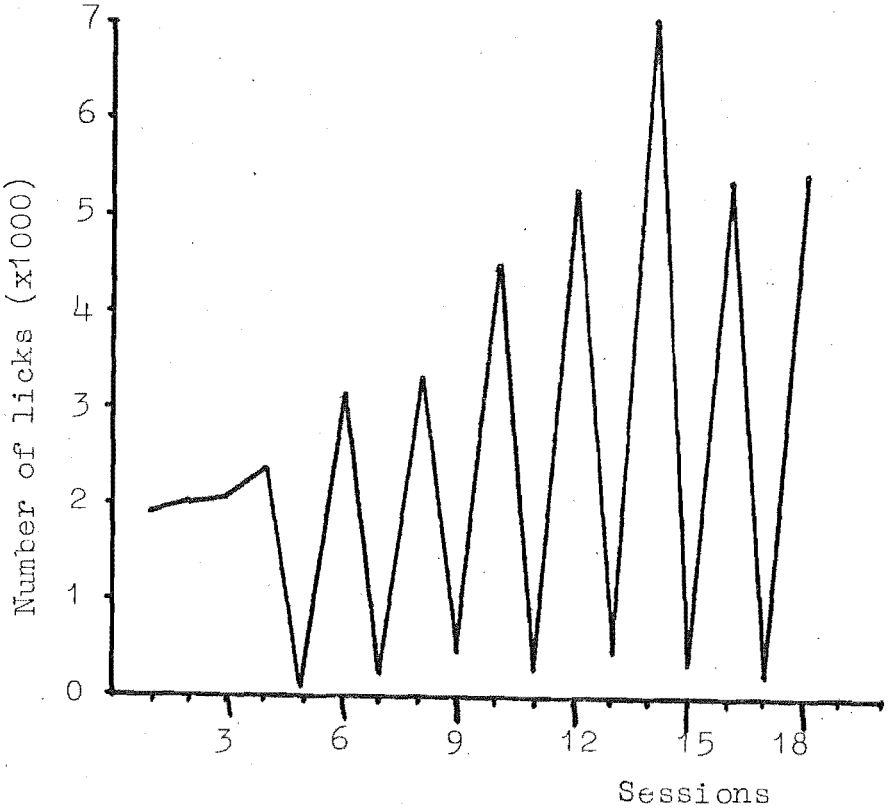
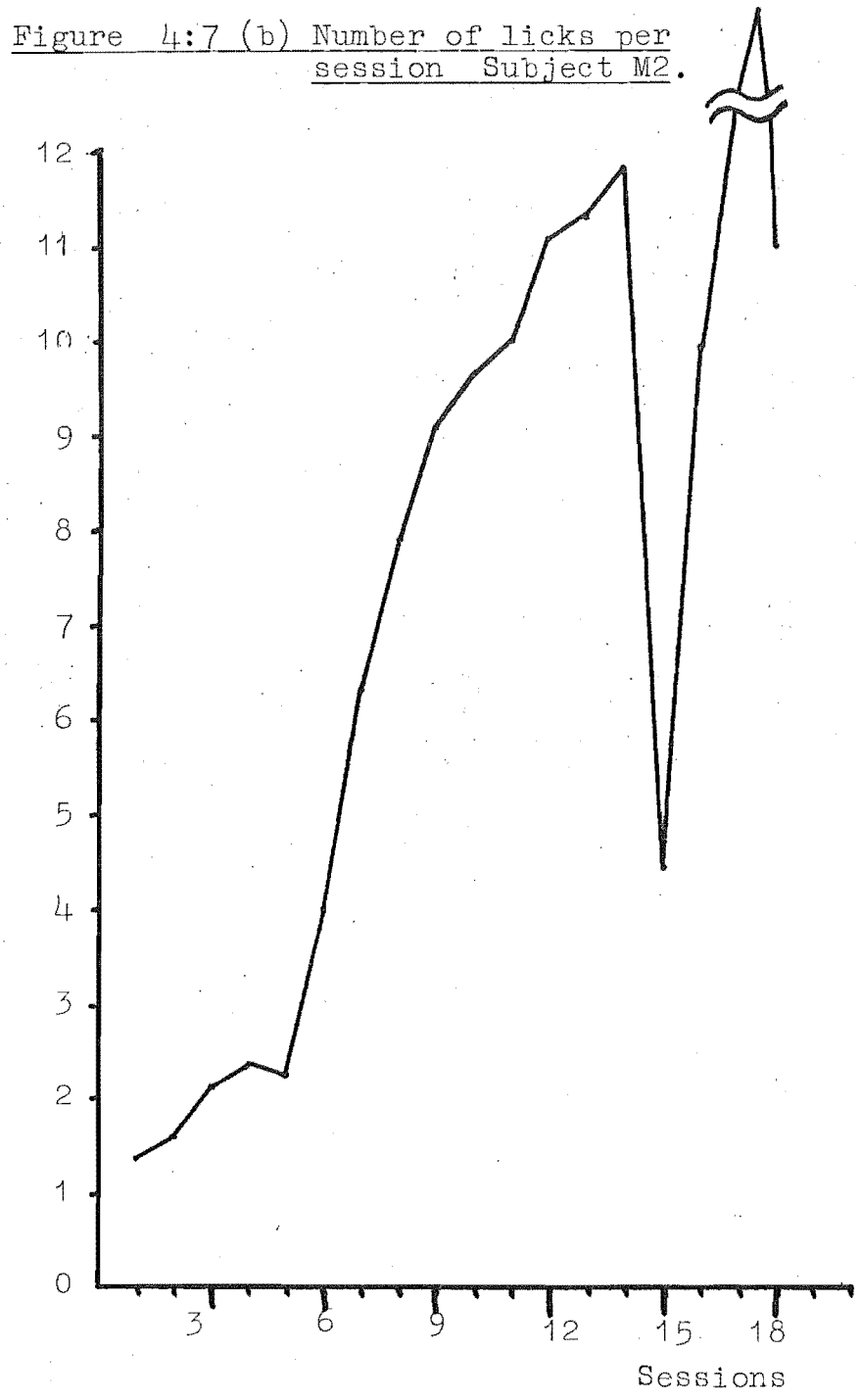


Figure 4:7 (b) Number of licks per session Subject M2.



the drinkometer was disconnected. Observations of the subjects every 50 minutes during session 20 indicated that they continued licking (notably subjects M1 and M2) although subject F1 did not make many contacts (as was expected with the lowered performance of this animal in previous sessions with the licking tube).

(d) Temporal Distributions of Drinking and Licking: These were derived by the same method as used in the pilot study, and are presented in Table 4.11 (drinking tube) and Table 4.12 (licking tube) and in Figures 4.8 a - c. A further analysis is presented by examining the within session distribution of drinkometer contacts for each tube according to grouped data based upon blocks of 20 cycles of food delivery (as was described in the pilot study). This data is presented in Figures 4.9 a - c, and is derived from the mean number of drinkometer contacts per 20 cycle block, for each tube condition.

Discussion:

(a) Water Intake: The decrease in daily home-cage water intake when the subjects were food deprived is as expected from the pilot study, and the literature on water intake. With regard to schedule-induced polydipsia, Figures 4.6 a - c clearly indicate that the subjects attained stable levels of water intake about the eight and tenth sessions, but that the level of polydipsia (approximately 100-200%) is not as high as that reported by Falk (1969) who cites levels of 340% - 400% as being common. Significantly, the home-cage intake did not return to normal levels on those days following sessions with the drinking tube (i.e.

Table 4.11: The Temporal Distribution of Drinkometer Contacts: Drinking Tube.

Subject	M1			M2			F1		
Session No.	14	16	18	14	16	18	14	16	18
Successive 5 Sec Intervals									
1	2	2	0	0	5	0	0	0	0
2	1	1	0	9	1	0	2	0	0
3	15	3	6	59	1	18	3	3	9
4	30	10	13	76	15	50	14	21	46
5	41	23	20	80	30	67	29	48	56
6	45	31	24	79	39	75	50	52	63
7	46	35	28	71	44	79	56	55	62
8	42	34	28	66	46	75	62	49	52
9	35	31	21	60	47	73	56	39	49
10	35	31	20	54	49	69	45	35	34
11	31	26	16	48	50	65	33	25	17
12	25	23	13	47	47	61	30	13	9
13	17	18	9	59	43	57	27	7	8
14	17	14	8	40	40	50	21	7	5
15	16	10	6	46	41	49	26	6	4
16	14	9	8	38	39	50	14	4	4
17	19	10	8	30	40	41	12	5	5
18	19	7	5	36	40	38	14	5	6
19	12	4	4	42	45	36	9	2	3
20	12	5	2	46	42	31	5	7	5

Table 4.12: The Temporal Distribution of Drinkometer Contacts: 'Licking Tube.

Subject	M1			M2			F1		
Session No.	13	15	17	13	15	17	13	15	17
Successive 5-sec Intervals									
1	0	1	0	4	1	7	0	1	0
2	1	0	0	13	0	1	0	1	0
3	5	9	6	61	3	33	0	0	0
4	11	19	10	77	14	68	9	1	2
5	21	29	14	58	25	66	9	3	4
6	12	26	18	46	22	68	12	7	3
7	8	21	20	43	23	66	6	4	3
8	10	15	25	42	32	62	9	7	8
9	13	18	23	47	25	57	6	5	4
10	6	18	16	45	23	52	4	4	4
11	13	21	8	49	22	67	6	2	1
12	15	16	11	46	21	64	5	3	1
13	14	13	12	57	25	64	1	4	2
14	15	14	11	45	22	64	1	6	2
15	10	10	13	48	25	63	2	4	0
16	15	13	11	54	23	67	3	3	0
17	10	18	17	45	21	63	6	2	0
18	12	13	16	48	23	57	1	2	0
19	7	8	17	51	21	66	5	1	0
20	5	17	14	60	15	71	1	1	0

Figure 4:8 (a) Temporal distribution: Subject M1 drinking tube.

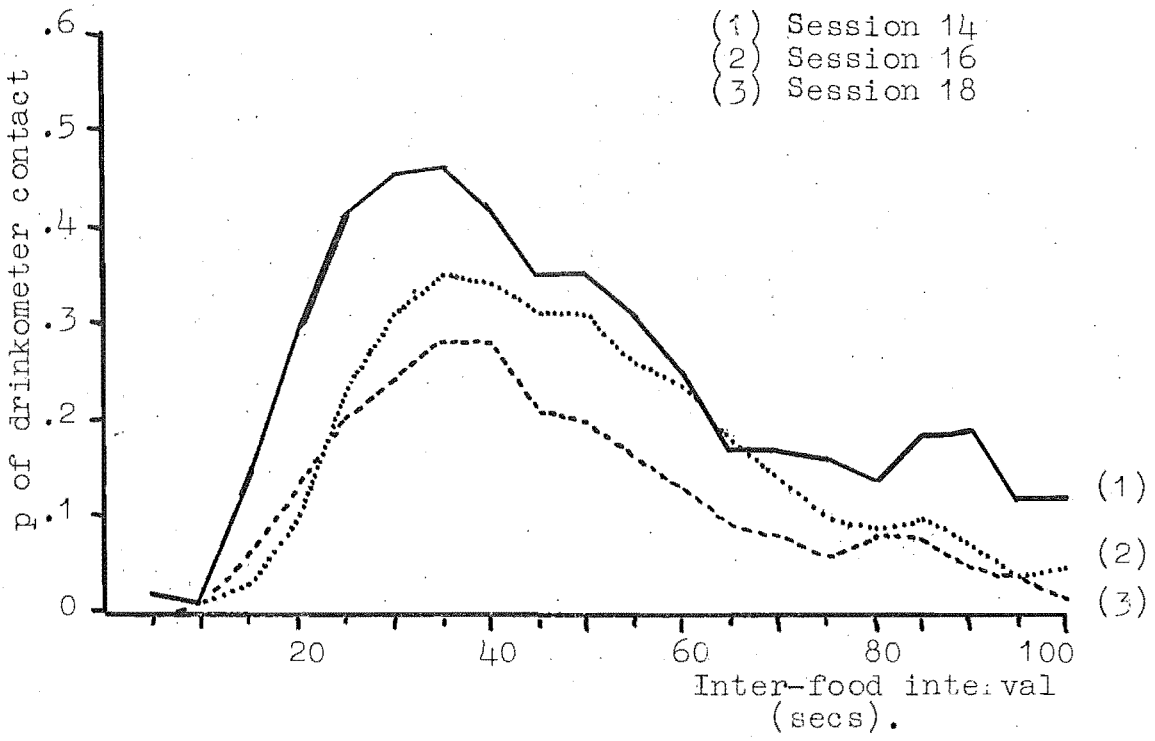


Figure 4:8 (a) Temporal distribution: Subject M1 licking tube.

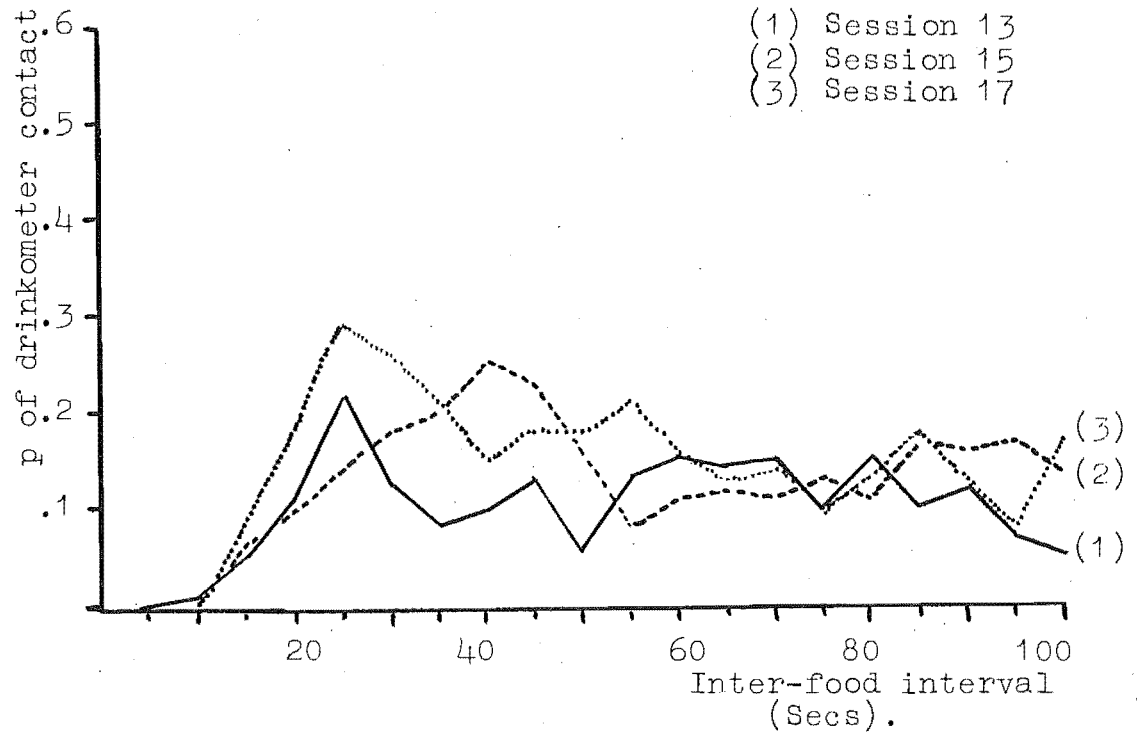


Figure 4:8 (b) Temporal distribution: Subject M2 drinking tube.

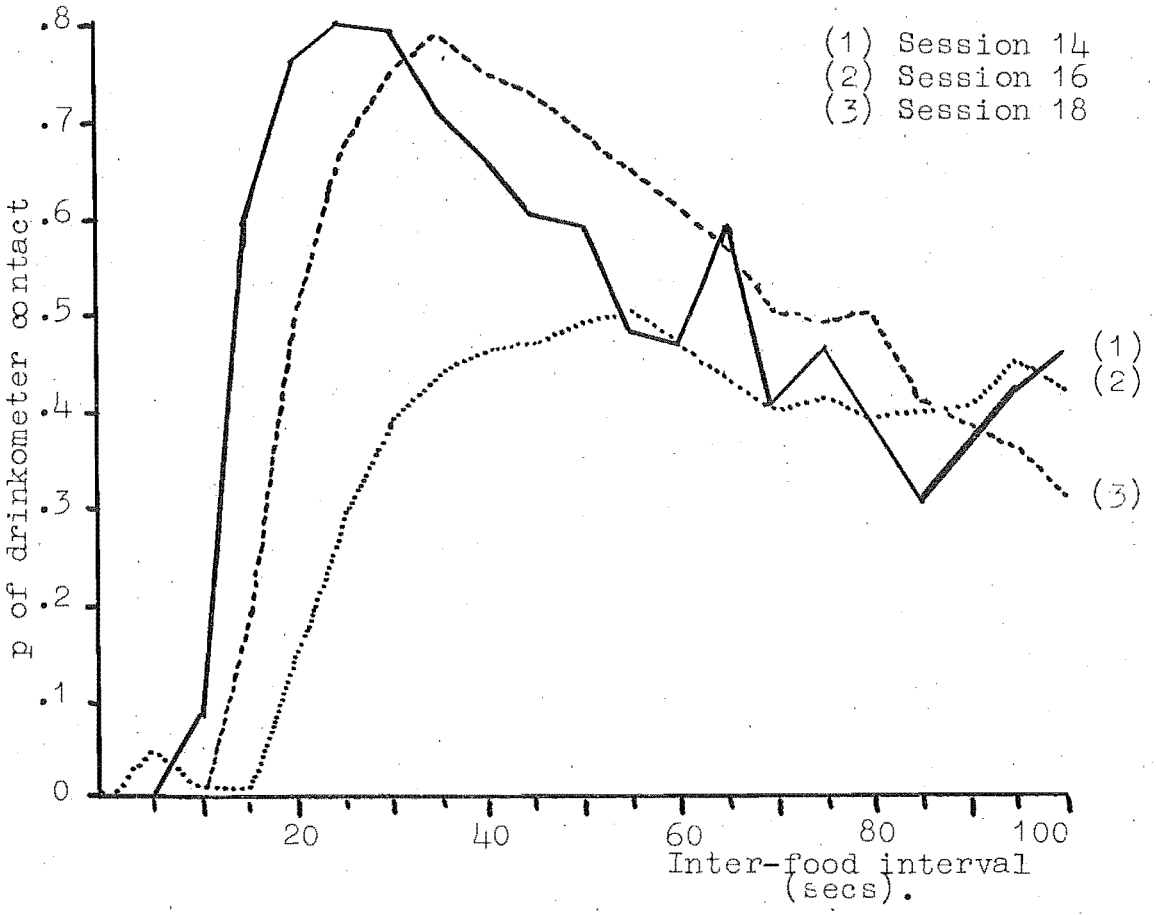


Figure 4:8 (b) Temporal distribution: Subject M2 licking tube.

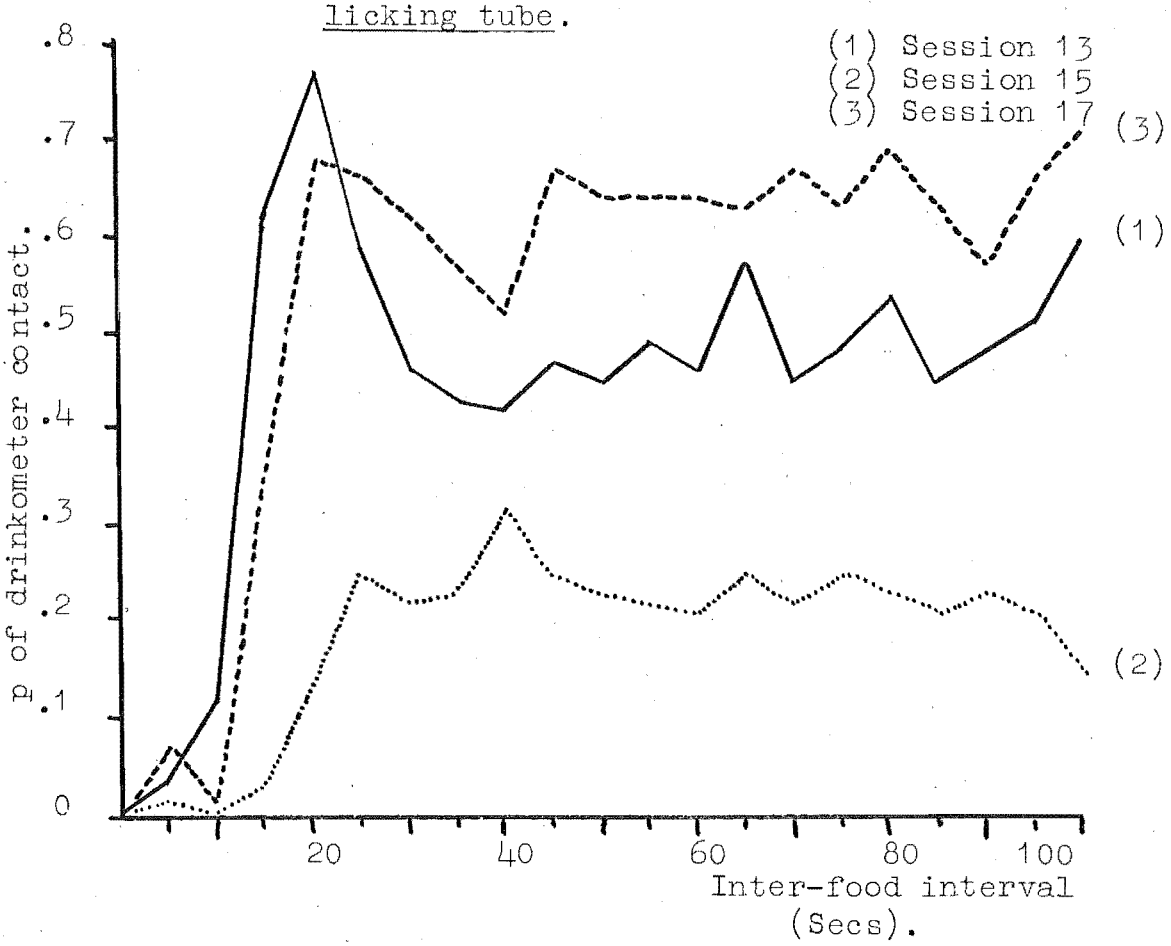


Figure 4:8 (c) Temporal distribution: Subject F1 drinking tube.

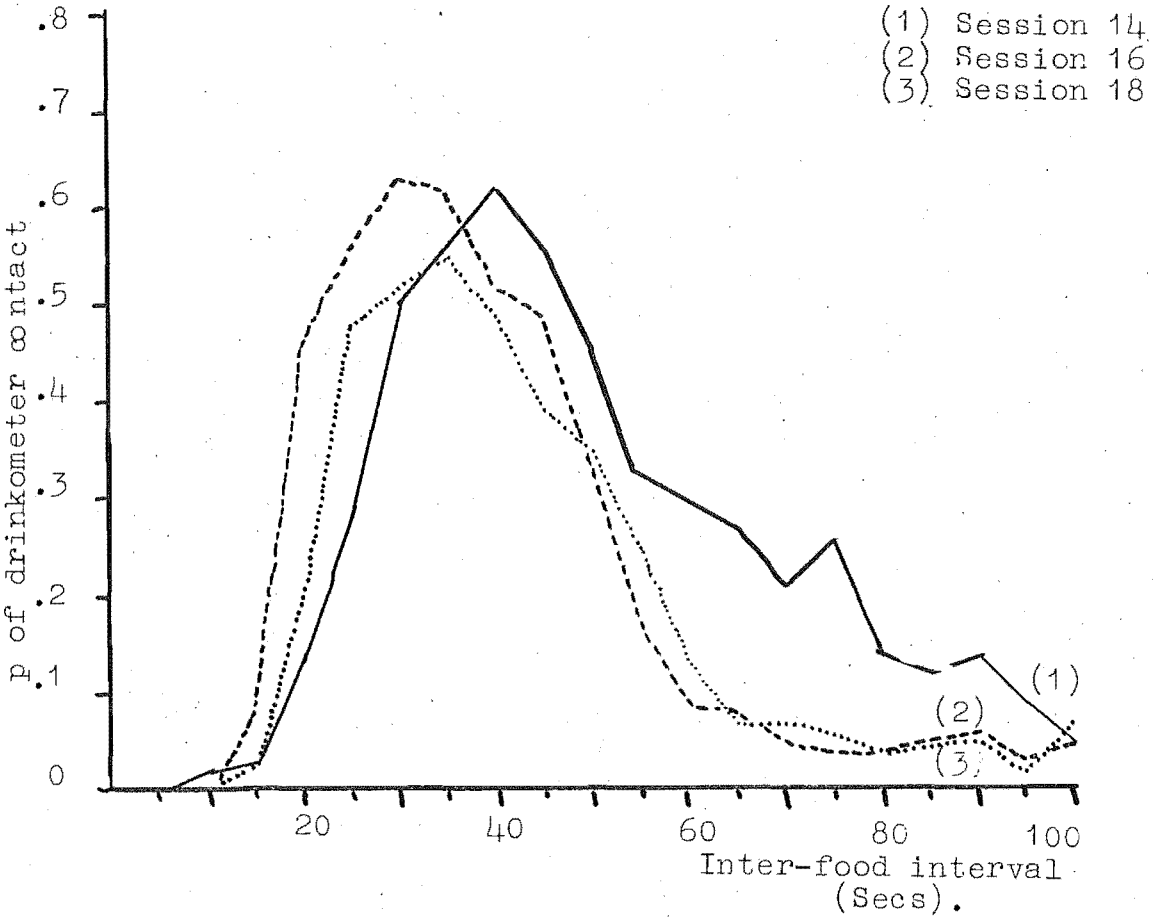


Figure 4:8 (c) Temporal distribution: Subject F1 licking tube.

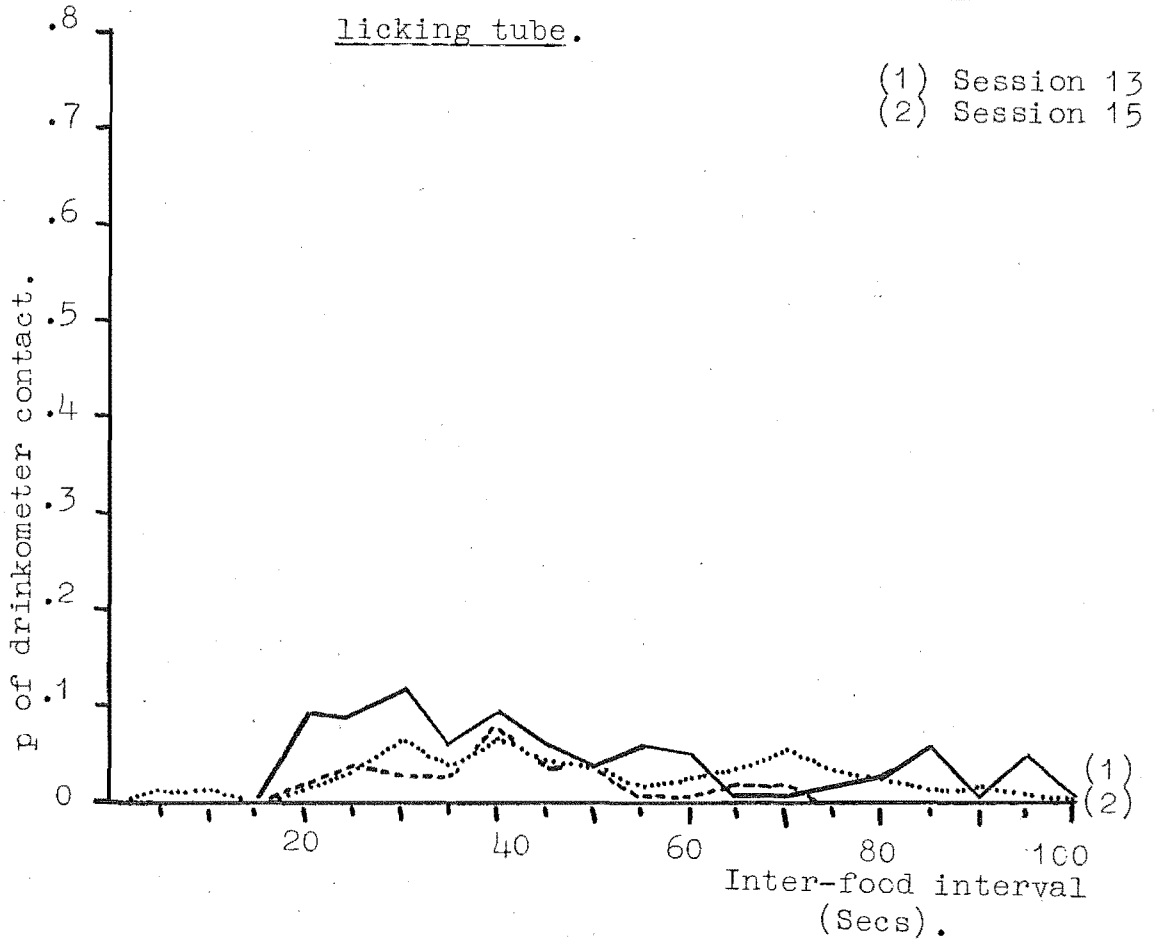


Figure 4:9 (c) Mean percentage drinkometer contacts per 20 cycles of food delivery Subject F1.

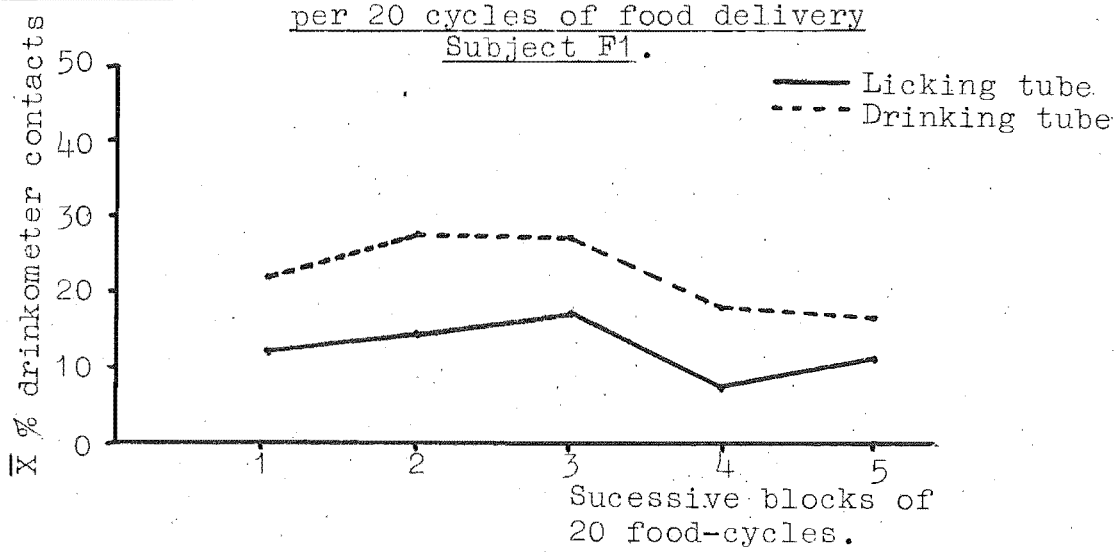


Figure 4:9 (a) Mean percentage drinkometer contacts per 20 cycles of food delivery Subject M1.

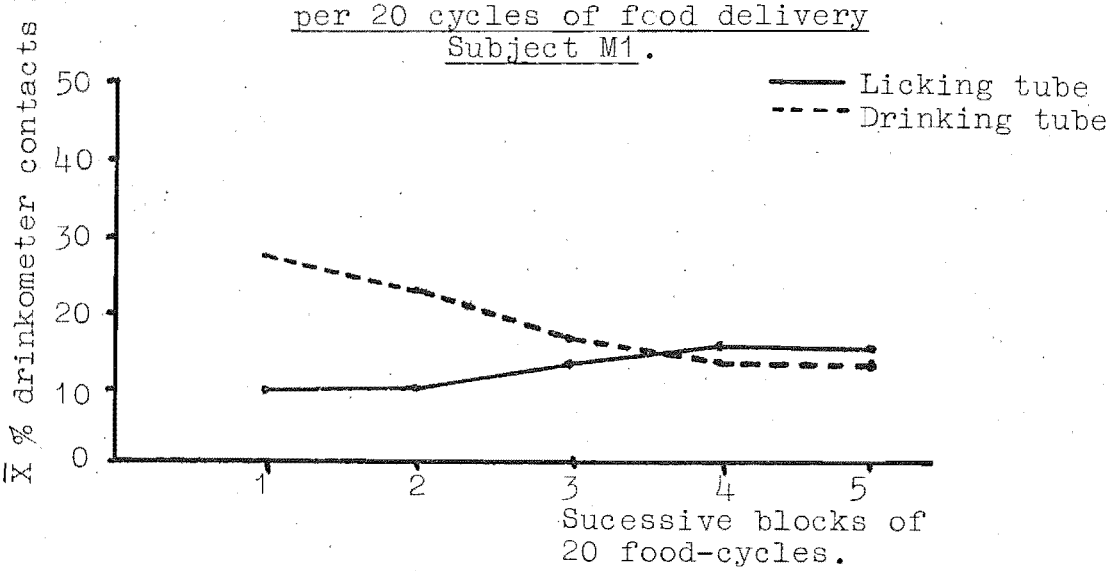
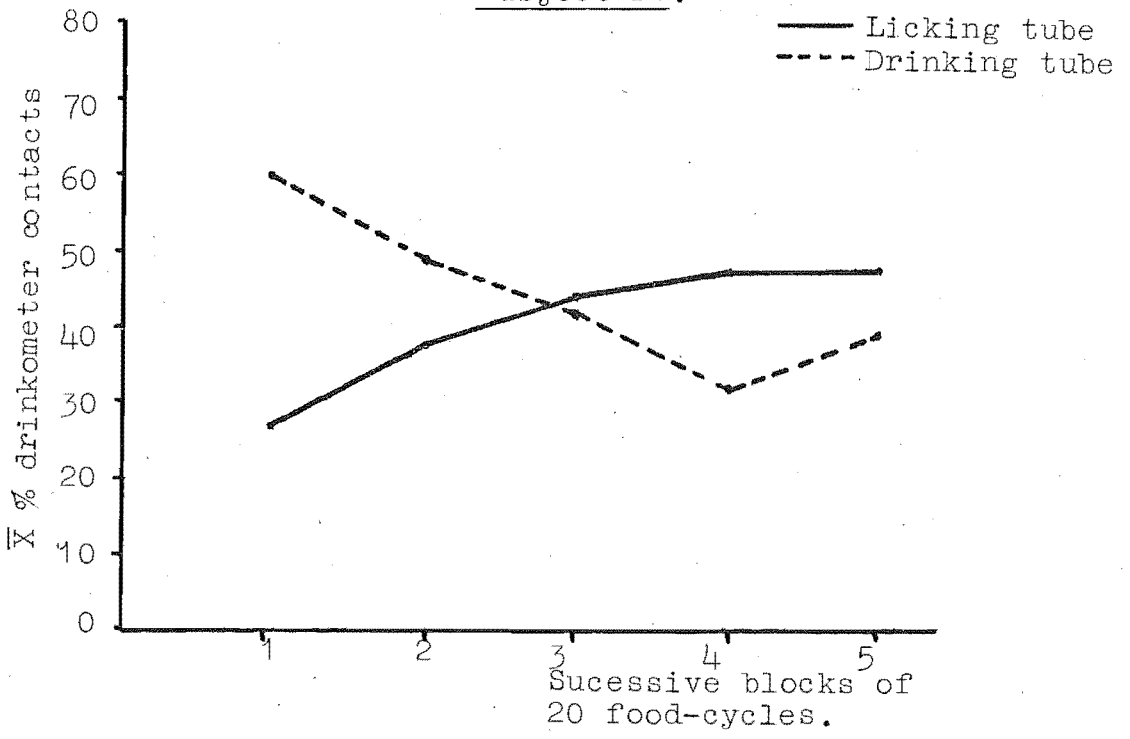


Figure 4:9 (b) Mean percentage drinkometer contacts per 20 cycles of food delivery Subject F1.



when the subjects were polydipsic) and indicates that the subjects require greater than 48 hours to excrete the excess liquid and regain normal functioning. This finding is in accordance with the physiological evidence of considerable overhydration as determined by plasma and muscle water, hematocrit, and plasma protein measures. The performance of subject M2 on session 15 reflects the results of the excessive drinking, as this animal consumed 43 ml's of water, exhibited a marked piloerection, and appeared generally sick at the end of the session and throughout the next day (as is indicated by the reduction in number of licks on session 16).

(b) Number of Licks: From Figures 4.7 a - c it can be seen that considerable individual differences exist in the magnitude of licking recorded on the respective tubes. Subjects F1 and M1 showed reduced responding to the licking tube, but stable polydipsia on the other, while M2 followed the pattern of the pilot study subject with high rates of responding on both tubes. These data lend support to Segals' observations that there are wide variations between subjects in licking rates and in the effectiveness and consequences of licking (i.e. whether little or considerable water is consumed).

(c) Control Sessions: The data from these sessions indicate that the subjects continued to respond to a similar level as the experimental sessions (when the drinkometer was connected). However, these findings are eqivocal on two grounds:

(a) it may be hypothesized that possible rewarding current effects were present only in the lick-

ing tube condition (and that the adjunctive behaviour was under the control of the water-ingestion response in the drinking tube condition). Consequently the control sessions would not accurately reflect likely current effects if the data from the drinking tube condition were considered (i.e. the amount of water consumed.)

(b) there may have been too few control sessions for extinction effects to become evident, thereby indicating the role of rewarding current effects.

From the literature it is evident that polydipsia cannot be attributable to rewarding current effects (eg. Falk, 1969), but the anomolous findings from the licking tube cannot be discounted as being due to this factor.

(d) Temporal Distribution of Drinking and Licking: The temporal distributions reflect the individual differences noted in the number of licks recorded under each tube condition, and consequently require separate consideration.

(1) The drinking tube distributions: These indicate that the maximum probability of contact with the drinkometer occurs early in the interfood interval (approximately between 20 and 40 seconds) but that there is some responding throughout the remainder of the interval, especially in the case of M2. As with the pilot study, the probability of drinkometer contact is virtually zero in the first few seconds of the interval, when the animal is engaged in eating. The individual session curves show an overall similarity in shape and magnitude for each subject.

However, despite the fact that the maximum probability of drinkometer contact occurs early in the interval, the results do not support an exclusively "postpellet phenomenon" description for polydipsia.

(2) The Licking Tube Distributions: The distributions obtained with this tube reflect the lower levels of responding recorded by subjects F1 and M1 under this experimental condition. The distributions obtained from these two subjects indicate that responding occurs with approximate equi-probability throughout the interfood interval. The distribution for M2 follows the pattern of the pilot study, with a high probability of responding over the bulk of the interfood interval. As with the drinking tube condition, all subjects showed minimal responding at the point of food delivery, as would be expected of food deprived rats.

(3) Within Session Features: The data displayed in Figures 4.9 a - c show that the mean percentage of drinkometer contacts diminish across the session length for the drinking tube condition, and imply that satiation occurs in polydipsia. The drinkometer contacts with the licking tube show an increase across the session (except for F1 who exhibited negligible responding under this conditon anyhow) and support the findings in the pilot study. Since the subjects do not consume water in this condition, satiation effects are not to be expected, and the increase in drinkometer contacts over the session may reflect an increase of the underlying motivational factors that govern this behaviour (i.e. an increase in the "arousal" or "thwarting" factors associated with adjunctive

behaviour, that may decrease when the subject engages in consummatory activities such as drinking, wheel-running etc). This hypothesis would support a view of responding to the licking tube as being a product of the incompleted drinking response, rather than being the result of a separate response topography. However, the nature of this experiment precludes any further evaluation of this hypothesis, and it must remain as speculative.

General Discussion:

The results of this experiment confirm that rats will persistently lick at a tube that does not permit drinking, but also indicate that this response is subject to individual differences. From these results it is possible to discount two potential explanations for this behaviour, namely:

(1) idiosyncracy on the part of the pilot study subject (all subjects responded to some degree).

(2) lack of spatial discrimination between the different tubes (each tube had a separate location in the experimental situation).

Furthermore, the control sessions data imply that rewarding drinkometer current effects may also be discounted, although these findings are eqivocal. It has not been possible to investigate schedule-induced tongue cooling effects, nor has the potential role of two separate topographies been evaluated, largely because of the nature of the experimental paradigm used.

The temporal distribution obtained with polydipsia challenges the "immediate post-pellet" description of this

phenomenon, although the bulk of the responding does occur early in the interfood interval. Where responding to the licking tube occurs to some magnitude, the temporal distribution of drinkometer contacts follows a similar distribution to polydipsic responses, with the added difference that there are usually more responses late in the interfood interval.

The pattern of responding tends to slowly diminish over the session length with polydipsia (implying that satiation effects are operating) while the responding to the licking tube tends to increase over the session length (implying an increase in the underlying motivational factors operating in this situation). This difference in within-session performance might be evidence of either the existence of two separate response topographies, or that the licking (without water) topography is a subsidary response of adjunctive polydipsia behaviour that operates in the absence of liquid ingestion and thereby increases in strength due to the absence of the consumatory drinking response. This possibility suggests the need for an extension of this experiment, with some test of preference for the respective tubes, as well as a further examination of the temporal distributions of responding.

(D) Experiment 3: A Further Comparison of the Drinking and Licking Topographies.

The previous experiment suggested the need for a repetition of the procedure, with an assessment of a possible preference for one tube over the other. This

issue bears reference to the adaptiveness of schedule-induced polydipsia as a biological event. Falk (1972) has considered the adjustive ends served by polydipsia (and adjunctive behaviours generally) to which he comments,

> "The question as to whether adjunctive behaviour is a toxic manifestation or a creative deviation cannot be answered by a description of the topography of the response. If the adjunctive behaviour results in the organism failing to adjust to environmental contingencies, or if the behaviour itself leads to damaging consequences, then it can be considered as maladaptive or as a toxic response. If the behaviour results in a new behavioural emphasis working to the benefit of the organism, then it can be viewed as a powerful mechanism for adaptive change. Whether the result is toxic or creative will be a function not only of the generator schedule but also of the environmental circumstances - the ecology of the situation".

This statement focuses upon the apparent physiological maladaptiveness of schedule-induced polydipsia, since the animal expends considerable energy consuming, processing, and expelling water through its body, although it is already in a state of depleted

energy reserves because of food deprivation. The water is consumed at room temperature, and expelled at body temperature, with a consequent energy loss of some magnitude. Furthermore, the animal may attain a physiological state of water intoxication and cellular overhydration, to which one might impute some degree of aversiveness, since the animal does not attain this state under normal conditions. Therefore, given a simultaneous choice of two seemingly similar topographies, one of which has a marked physiological cost in terms of energy balance, it might be expected that the subjects would show a preference for the alternate(less expensive) behaviour; i.e. the licking topography. A converse hypothesis may also be entertained, in which a preference for the drinking tube would indicate the role of the "full blown" consummatory response of drinking in schedule-induced polydipsia, with the licking tube behaviour representing an incomplete response that leaves the underlying motivational factors in a state of unfulfilment.

Subjects:

2 male and 1 female experimentally naive hooded rats aged 195 days served. The subjects individually weighed 278 grams (M3), 296 grams (M4), and 214 grams (F2). They were individually caged for 14 days prior to being food deprived to 80% free-feeding weight. Housing and feeding were similar to Experiment 2.

Apparatus:

The same apparatus was used as in Experiment 2.

Procedure:

A similar procedure was adpoted as in Experiment 2 with some minor variations. Home-cage water intake at 100% and 80% free-feeding weight was individually recorded for 7 days per condition. The experimental sessions were identical to Experiment 2 until sessions 17 and 18, on which occasions both the drinking and licking tubes were simultaneously present. Days 19 - 24 were control sessions with the drinkometer disconnected, the drinking tube being present on days 19, 21 and 23, while the licking tube was present on days 20, 22 and 24. Control sessions data was obtained in the same manner as in Experiment 2.

Results:

(a) Water Intake: The mean daily intakes for 7 days at 100% and at 80% free-feeding weight are given in Table 4.13, and indicate the previously observed decrease in daily water intake with food deprivation. The water intake during the experimental sessions is given in Table 4.14, and comprises home-cage, experimental session, and total intake data. The daily total intake is also presented in Figures 4.10 a - c.

The experimental sessions intake show a stable level of schedule-induced polydipsia developing and reaching asymptote about session eight. The level of polydipsic intake recorded at asymptote was in the order of 300-400% of the daily intake for each subject at 80% free-feeding weight. As with Experiment 2, the daily intakes were depressed on days following sessions with

Table 4.13: Pre-experimental Daily Water Intake (ml's)

	100% Free-Feeding Weight								80% Free-Feeding Weight							
Days	1	2	3	4	5	6	7	Mean	1	2	3	4	5	6	7	Mean
M3	12.6	14.2	9.6	8.1	11.3	13.7	12.2	11.6	6.5	4.2	8.1	7.0	6.1	8.3	9.3	7.1
M4	15.3	11.8	10.4	7.2	12.1	9.8	9.6	10.9	4.9	7.5	6.9	8.1	5.8	9.8	6.1	7.0
F2	6.1	7.8	6.9	9.8	8.1	11.8	10.4	8.7	3.1	4.9	- Tube broken before record-ing	6.1	5.4	5.6	4.8	4.9

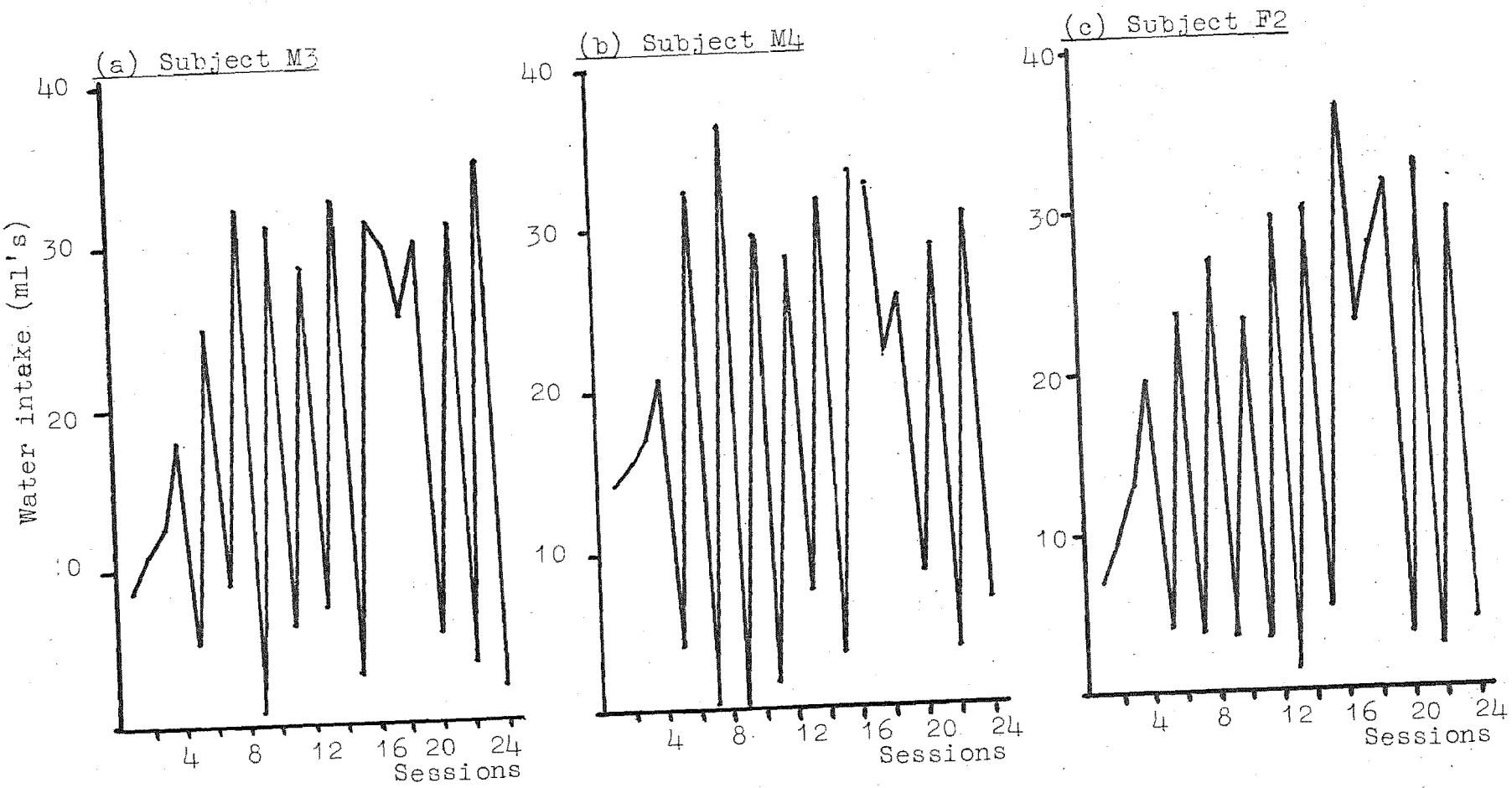
Table 4.14: Daily Water Intake (ml's)

		M3			M4			F2		
Days	Experimental condition	H/C	Exp.	Total	H/C	Exp.	Total	H/C	Exp.	Total
1	D	6.4	1.8	8.2	11.7	3.4	14.1	6.6	0.3	6.9
2	D	2.6	7.9	10.5	7.3	8.1	15.4	8.1	1.4	9.5
3	D	0.3	11.8	12.1	4.1	12.8	16.9	3.4	9.6	13.0
4	D	0.0	17.6	17.6	0.7	19.9	20.6	0.8	18.5	19.3
5	L	5.1	-	5.1	4.1	-	4.1	4.0	-	4.0
6	D	2.4	21.8	24.2	3.7	28.4	32.1	2.1	21.4	23.5
7	L	8.6	-	8.6	0.4	-	0.4	3.7	-	3.7
8	D	0.0	31.5	31.5	6.8	30.3	37.1	0.9	25.7	26.6
9	L	0.7	-	0.7	0.0	-	0.0	3.3	-	3.3
10	D	1.1	29.4	30.5	2.7	26.8	29.5	1.8	21.2	23.0
11	L	5.9	-	5.9	1.8	-	1.8	3.4	-	3.4
12	D	2.7	25.3	28.0	0.5	27.5	28.0	7.1	22.3	29.4
13	L	7.0	-	7.0	7.6	-	7.6	1.3	-	1.3
14	D	0.3	31.8	32.1	4.2	27.5	31.7	6.8	24.6	31.4
15	L	2.8	-	2.8	3.5	-	3.5	5.2	-	5.2
16	D	0.9	29.7	30.6	7.4	25.9	33.3	4.4	31.8	36.2
17	LD	0.7	28.4	29.1	1.4	31.1	32.5	0.2	22.7	22.9
18	LD	1.0	23.9	24.9	0.0	21.9	21.9	3.8	23.9	27.7
19	D*	1.4	28.2	29.6	0.8	24.6	25.4	1.9	29.4	31.3
20	L*	5.1	-	5.1	8.3	-	8.3	3.6	-	3.6
21	D*	2.9	27.4	30.3	3.0	25.7	28.7	2.4	30.2	32.6
22	L*	3.3	-	3.3	3.6	-	3.6	2.7	-	2.7
23	D*	1.7	32.6	34.3	2.9	27.5	30.4	1.8	27.9	29.7
24	L*	1.9	-	1.9	6.6	-	6.6	4.2	-	4.2

* Drinkometer disconnected
H/C Home-cage intake
Exp. Experimental Chamber Intake
Total Total Intake

D = Drinking Tube
L = Licking Tube

Figure 4:10 Daily water intake (ml's).



the drinking tube (i.e. polydipsic conditions).

(b) Number of Licks: The number of licks recorded reached asymptote about session 8 (in parallel with the water intake), but unlike the findings of Experiment 2, remained at this level throughout the following experimental sessions (irrespective of which tube was present). The number of licks per session are presented in Table 4.15 and in Figures 4.11 a - c. The curves described by these data are of similar slope and magnitude for all subjects (unlike those of Experiment 2).

(c) Simultaneous Choice Situation: The data from sessions 17 and 18 require separate evaluation as the two tubes were simultaneously present.

(I) Water Intake: The water intake for each subject under this condition reveal a slight decrease in the level of polydipsia obtained (of the order of 3-5 mls), but still show a significant level of polydipsia (as compared to daily home-cage levels of drinking).

(II) Number of Licks: Table 4.16 presents data on the number of licks recorded on each tube in the simultaneous choice situation, as well as comparative data from the other two experimental conditions (drinking tube and licking-tube-only). From this table it can be seen that:

(i) there are very few licks recorded on the licking tube (less than 2%) while high levels are recorded on the drinking tube. This indicates a clear preference for the drinking

Table 4.15: Number of Licks per Session

Session	Condition	M3	M4	F2
1	D	1904	2141	896
2	D	3882	3901	1684
3	D	5109	4714	3014
4	D	7495	5987	5962
5	L	6410	3477	2914
6	D	7386	7190	6841
7	L	7619	6338	6679
8	D	8990	8246	6487
9	L	7614	7748	6814
10	D	8141	8041	7098
11	L	7847	8113	8411
12	D	9408	7883	6984
13	L	9645	6464	9335
14	D	9164	7595	6764
15	L	7811	9834	5166
16	D	8341	8133	6947
17	LD	7356	8027	6794
18	LD	7312	7021	7312

Figure 4:11 Number of licks.

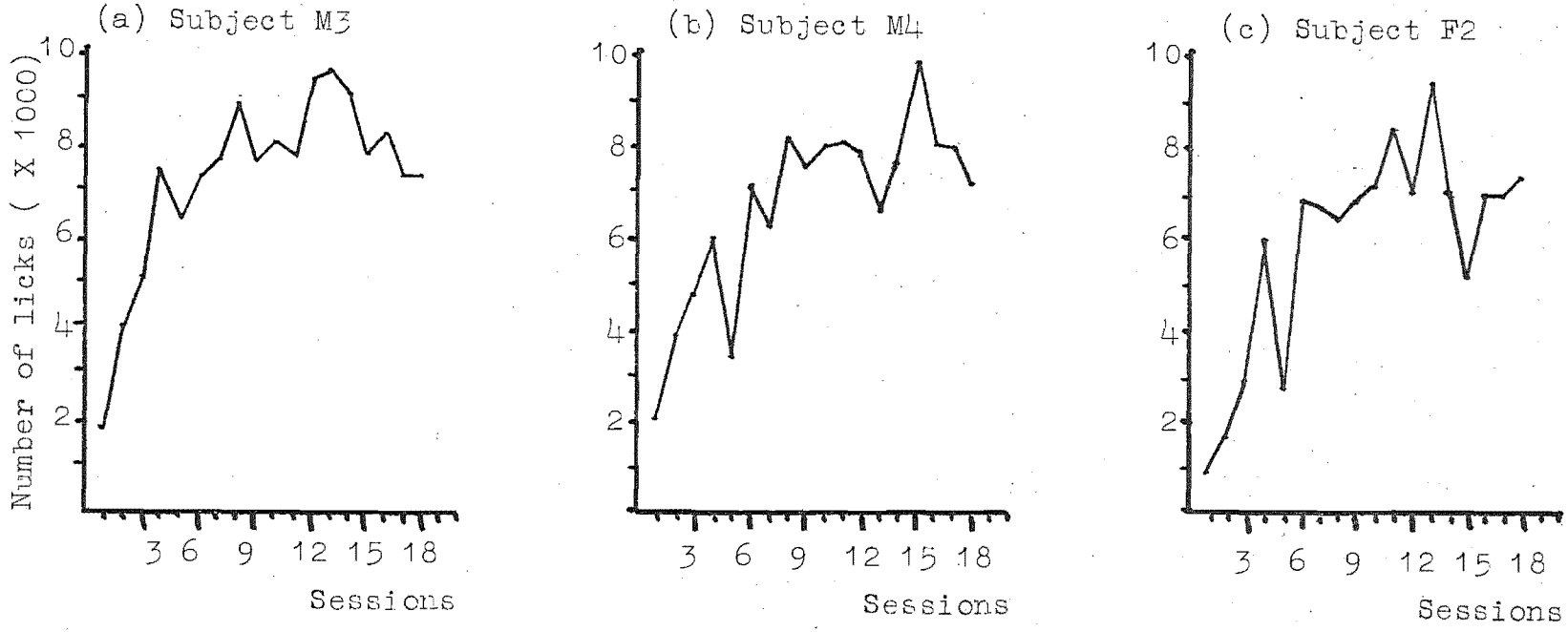


Table 4.16: Number of Licks per Experimental Session

	Licking Tube		Drinking Tube		Simultaneous Choice Condition	
					Licking Tube	Drinking Tube
M 3	Session 13	9645	Session 14	9164	Session 17 17	7339
	Session 15	7811	Session 16	8341	Session 18 93	7219
	Mean	8728	Mean	8752.5	Mean 55	7279
M 4	Session 13	6464	Session 14	7595	Session 17 147	7880
	Session 15	9834	Session 16	8133	Session 18 23	6998
	Mean	8149	Mean	7864	Mean 85	7439
F 2	Session 13	9335	Session 14	6764	Session 17 82	6712
	Session 15	5166	Session 16	6947	Session 18 93	7219
	Mean	7250.5	Mean	6855.5	Mean 87.5	6965.5

tube in a choice situation.

(ii) in the non-choice licking-tube-only condition, the number of licks recorded are equal or higher than those recorded on the drinking-tube-only condition, and are of a similar level to the number of licks recorded in the choice situation.

(d) Control Sessions: These sessions were conducted with the drinkometer connected and the data are comprised of:

(a) levels of water consumption for the drinking tube condition (sessions 19, 21, and 23).

(b) Observations as to whether the subjects continued to lick under the licking tube condition (sessions 20, 22 and 24).

The water intake data from sessions 19, 21 and 23 indicate the stable levels of polydipsia persisted in the absence of drinkometer recordings. Observational measures, taken at 50 minute intervals for a period of 5 minutes, indicated that the subjects continued to lick at high rates at the licking tube. No quantified measurements were taken during these sessions, but it appeared that the levels of licking were of the same order as those observed during the experimental sessions and confirmed the observations of Experiment 2.

(e) The Temporal Distribution of Drinkometer Contacts: The data presented were derived by the same method as used in Experiment 2. These are shown in Table 4.17 (licking tube), Table 4.18 (drinking tube) and Table 4.19 (simultaneous choice), and respectively present the

Table 4.17: Temporal Distribution of Drinkometer Contacts: Licking Tube.

Subject	M3		M4		F2	
Successive 5-sec Intervals	Session 13	Session 15	Session 13	Session 15	Session 13	Session 15
1	0	0	0	1	1	1
2	1	2	3	0	0	2
3	45	34	28	30	16	3
4	58	46	29	55	40	12
5	47	48	18	59	52	15
6	42	49	11	72	57	20
7	40	28	7	73	61	18
8	40	15	12	60	54	25
9	32	10	9	48	58	20
10	33	13	11	39	58	16
11	32	7	5	29	57	17
12	31	8	6	21	52	13
13	29	6	3	13	47	13
14	28	5	4	8	48	13
15	27	3	1	5	40	11
16	30	2	1	3	30	6
17	26	4	1	3	28	9
18	24	1	0	2	26	8
19	21	7	2	1	29	7
20	22	3	0	1	31	7

Table 4.18: Temporal Distribution of Drinkometer Contacts: Drinking Tube.

Subject	M3		M4		F2	
Successive 5-sec intervals	Sess.14	Sess.16	Sess.14	Sess.16	Sess.14	Sess.16
1	0	0	1	2	1	4
2	0	6	5	2	1	6
3	59	44	48	16	5	11
4	68	52	61	35	15	17
5	70	56	66	49	20	28
6	69	54	55	59	30	40
7	57	47	47	56	35	46
8	44	33	45	53	40	51
9	30	22	35	51	41	50
10	21	15	28	44	41	48
11	21	9	18	35	39	38
12	13	5	12	24	40	40
13	8	4	13	18	36	45
14	8	3	14	17	30	44
15	6	3	10	13	28	46
16	6	4	7	12	26	45
17	6	3	4	6	24	20
18	5	1	2	3	24	18
19	4	1	5	5	20	16
20	4	1	4	4	19	18

Table 4.19: Temporal Distribution of Drinkometer Contacts: Simultaneous Choice Situation.

Subject	M3						M4						F2					
	Session 17			Session 18			Session 17			Session 18			Session 17			Session 18		
	L	D	C	L	D	C	L	D	C	L	D	C	L	D	C	L	D	C
1	1	0	1	0	0	0	1	0	1	1	0	1	0	0	0	1	0	1
2	7	1	8	8	1	9	4	1	5	1	0	1	0	0	0	7	1	8
3	50	1	51	45	4	49	37	1	38	17	1	18	2	1	3	46	3	49
4	58	5	63	63	3	66	54	4	58	30	0	30	11	1	12	55	2	57
5	63	5	68	64	4	68	58	6	64	39	1	40	23	0	23	56	4	60
6	61	3	64	61	2	63	52	5	57	43	0	43	32	2	34	57	2	59
7	44	2	46	52	1	53	47	2	49	43	3	46	35	3	38	48	1	49
8	34	1	35	34	0	34	43	5	48	42	2	44	36	1	37	36	1	37
9	36	1	37	30	1	31	37	1	38	44	0	44	41	2	43	22	0	22
10	20	0	20	21	1	22	36	4	40	34	1	35	42	0	42	13	1	14
11	14	1	15	14	0	14	26	2	28	30	0	30	41	2	43	5	0	5
12	9	0	9	12	0	12	24	3	27	27	0	27	43	1	44	4	0	4
13	10	1	11	8	1	9	16	2	18	18	1	19	40	0	40	1	0	1
14	8	0	8	7	0	7	9	3	12	12	1	13	34	0	34	4	1	5
15	5	0	5	3	1	4	5	1	6	8	1	9	32	1	33	4	0	4
16	3	0	3	3	0	3	4	1	5	7	0	7	28	1	29	4	1	5
17	2	1	3	4	0	4	5	1	6	3	1	4	24	0	24	6	0	6
18	3	1	4	3	1	4	4	0	4	2	1	3	18	1	19	6	1	7
19	4	1	5	4	0	4	3	0	3	5	0	5	17	0	17	5	0	5
20	3	0	3	4	0	4	3	0	3	5	0	5	13	1	14	7	1	8

L : Licking Tube Distribution

D : Drinking Tube Distribution

C : Combined Distributions for both tubes.

distributions from each session for each subject. This information is further displayed in Figures 4.12 a - c (licking tube), 4.13 a - c (drinking tube) and 4.14 a - c (simultaneous choice).

As with Experiment 2, a within session analysis of the percentage of drinkometer contacts per block of 20 food cycles is presented, as is shown in Figures 4.15 a - c.

Discussion:

(a) Water Intake: The recorded decrease in daily consumption when food deprived confirms the previous findings in the pilot study and Experiment 2. The level of water intake that stabilised about session 8 (i.e. at asymptote) again reflects the findings of Experiment 2, and confirms the observations of Falk (1969).

Again, a delay in the return of home-cage water intake to normal levels, after polydipsic sessions, reflects the observations of Experiment 2, and reconfirms the long-term effects of polydipsia on the animals' physiological system.

(b) Number of Licks: The development of licking to asymptote, as shown in Figures 4.11 a - c, does not follow the pattern of Experiment 2, but may be accounted for in terms of the greatly increased levels of responding to the licking tube in this experiment by *all* animals. Unlike Experiment 2, where two of the subjects exhibited minimal licking on the licking tube, all the subjects in this study showed a vigourous response to this particular

Figure 4:12 (b) Temporal distribution of drinkometer contacts: Subject M4 licking tube.

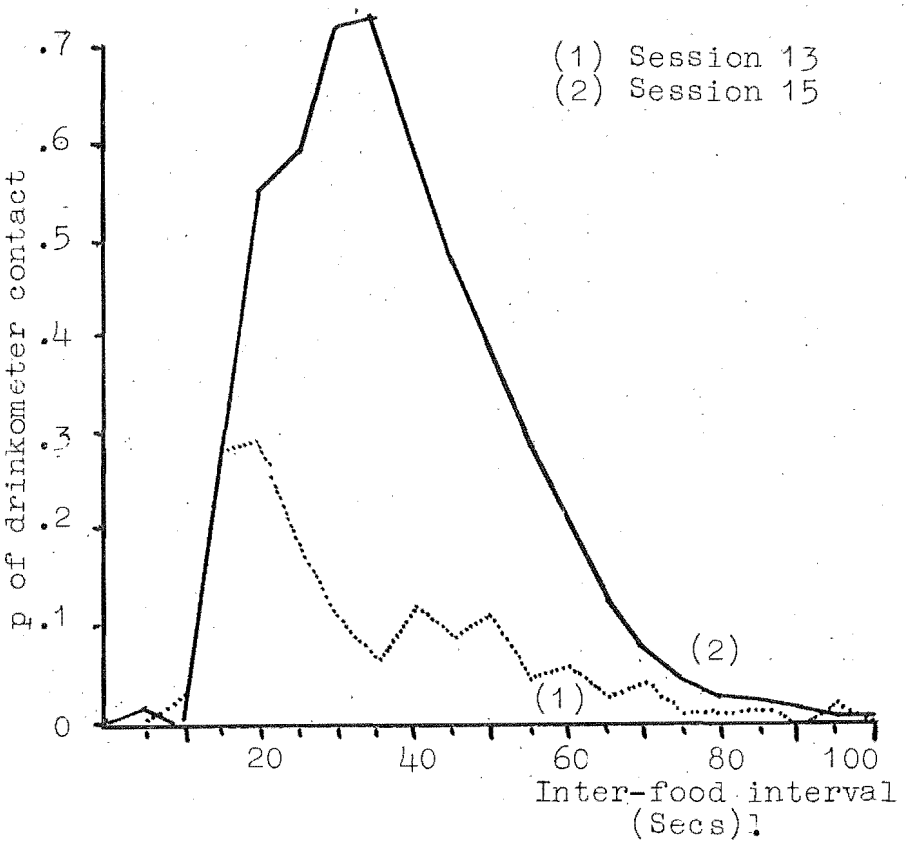


Figure 4:12 (a) Temporal distribution of drinkometer contacts: Subject M3 licking tube.

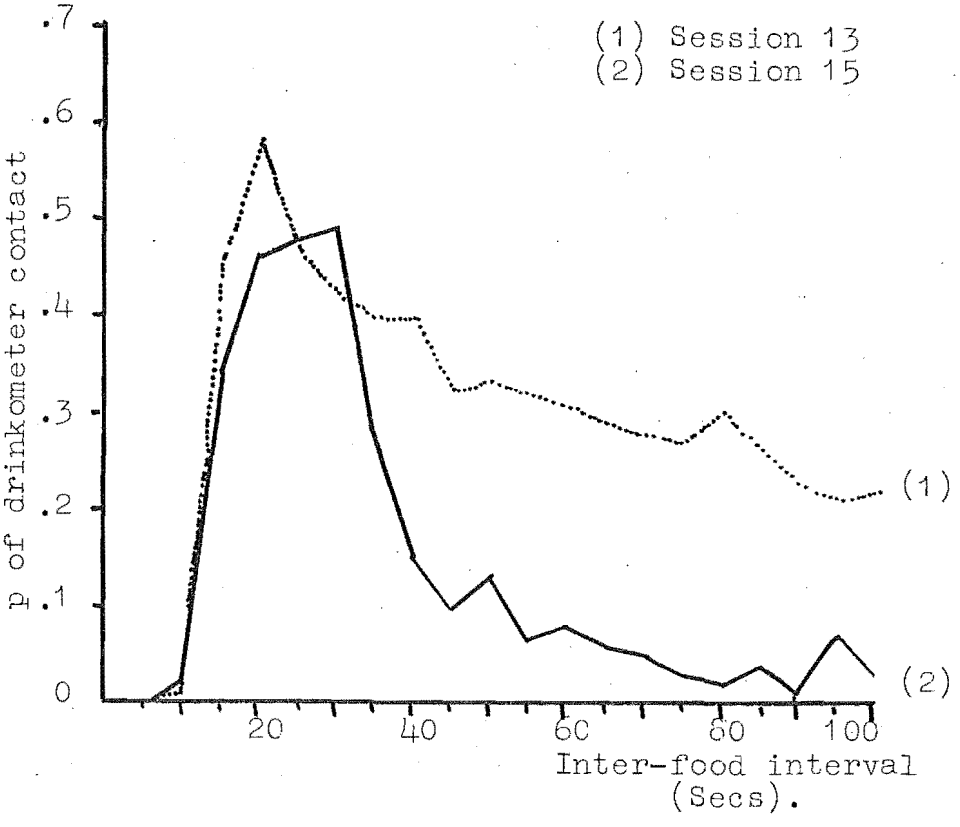


Figure 4:13 (b) Temporal distribution of drinkometer contacts: Subject M4 drinking tube.

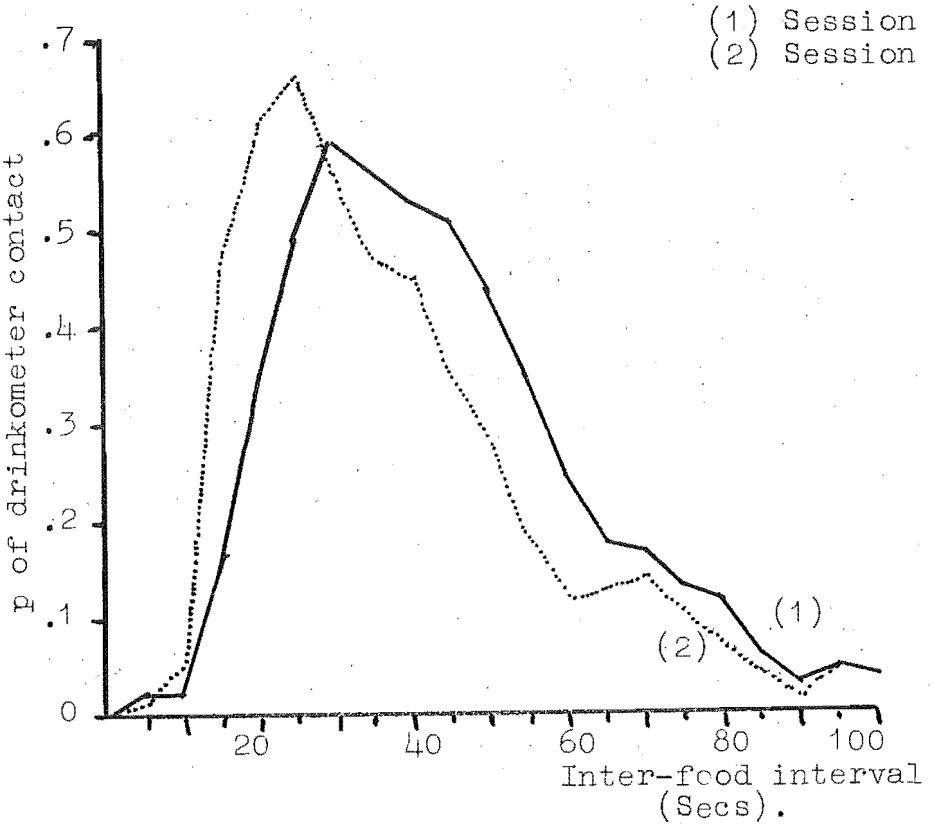


Figure 4:13 (a) Temporal distribution of drinkometer contacts: Subject M3 drinking tube.

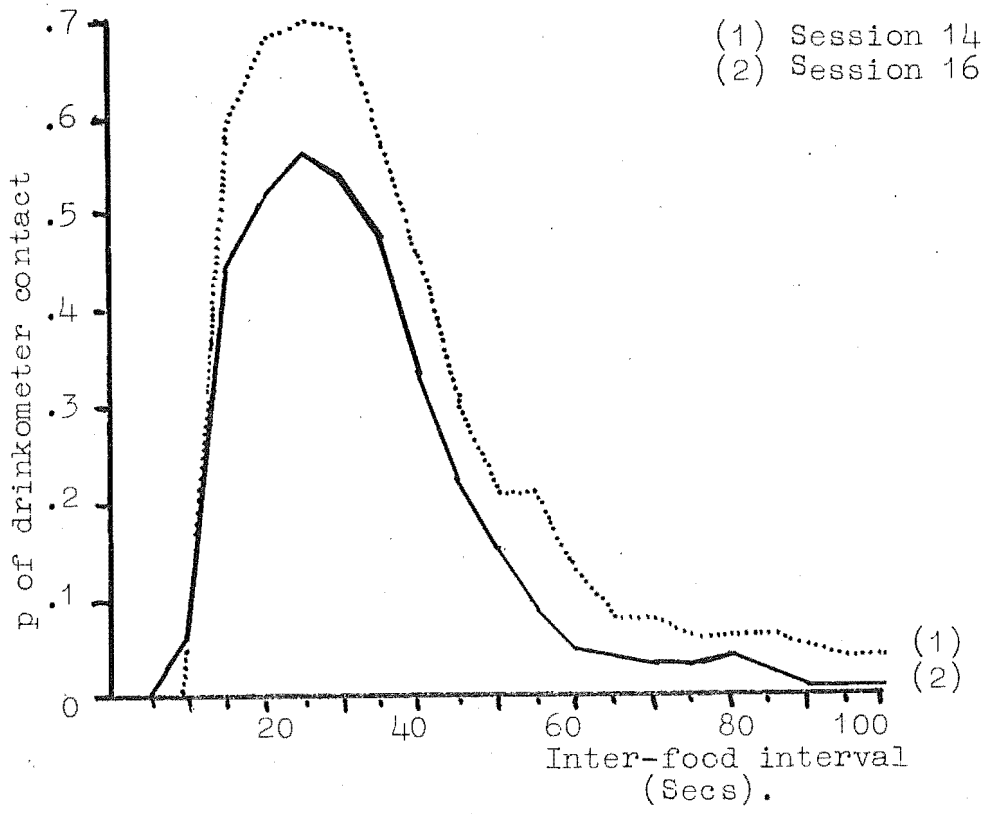


Figure 4:13 (c) Temporal distribution of drinkometer contacts: Subject F2 drinking tube.

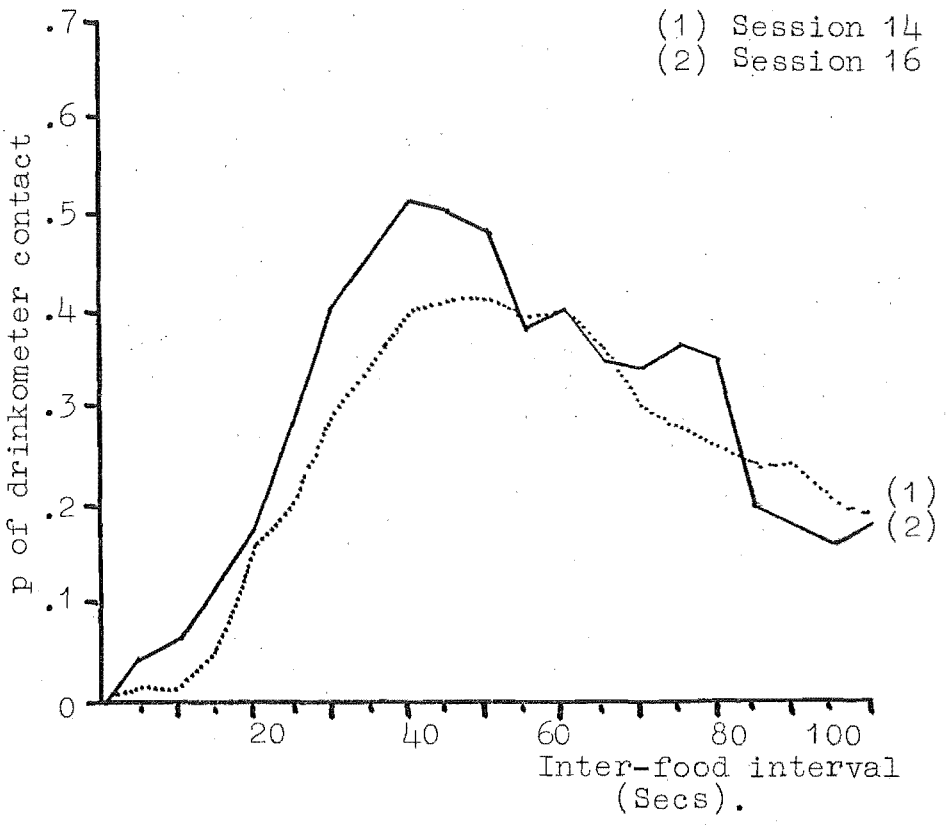


Figure 4:14 (a) Temporal distribution: Simultaneous choice condition. (Subject M3).

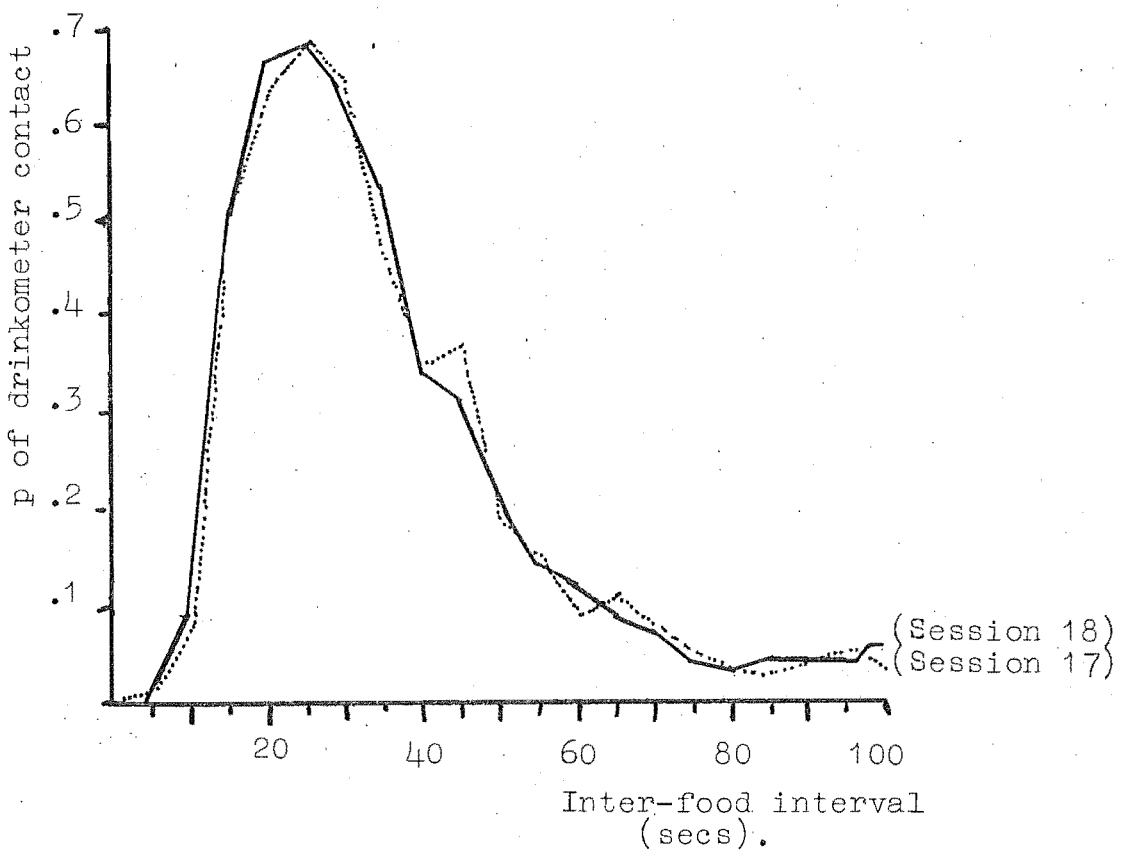


Figure 4:14 (b) Temporal distribution: Simultaneous choice condition. (Subject M4).

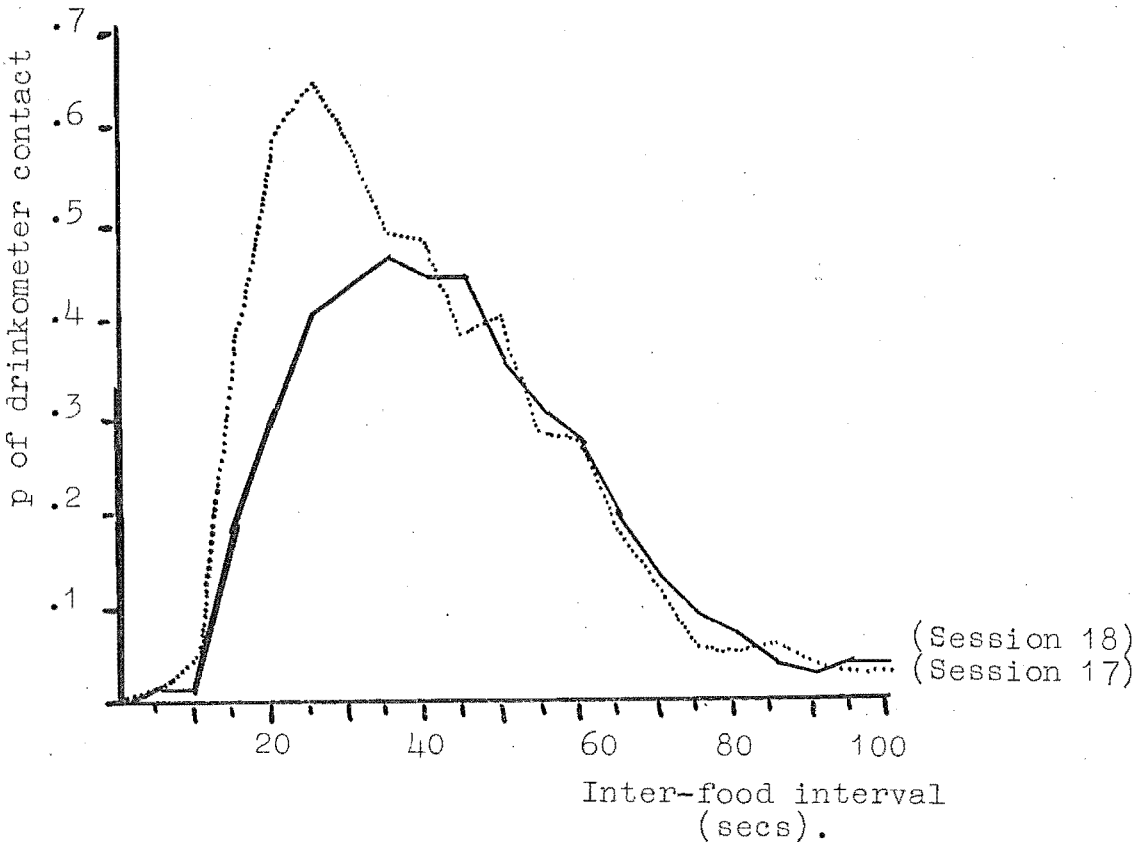


Figure 4:14 (c) Temporal distribution: Simultaneous choice condition. (Subject F2).

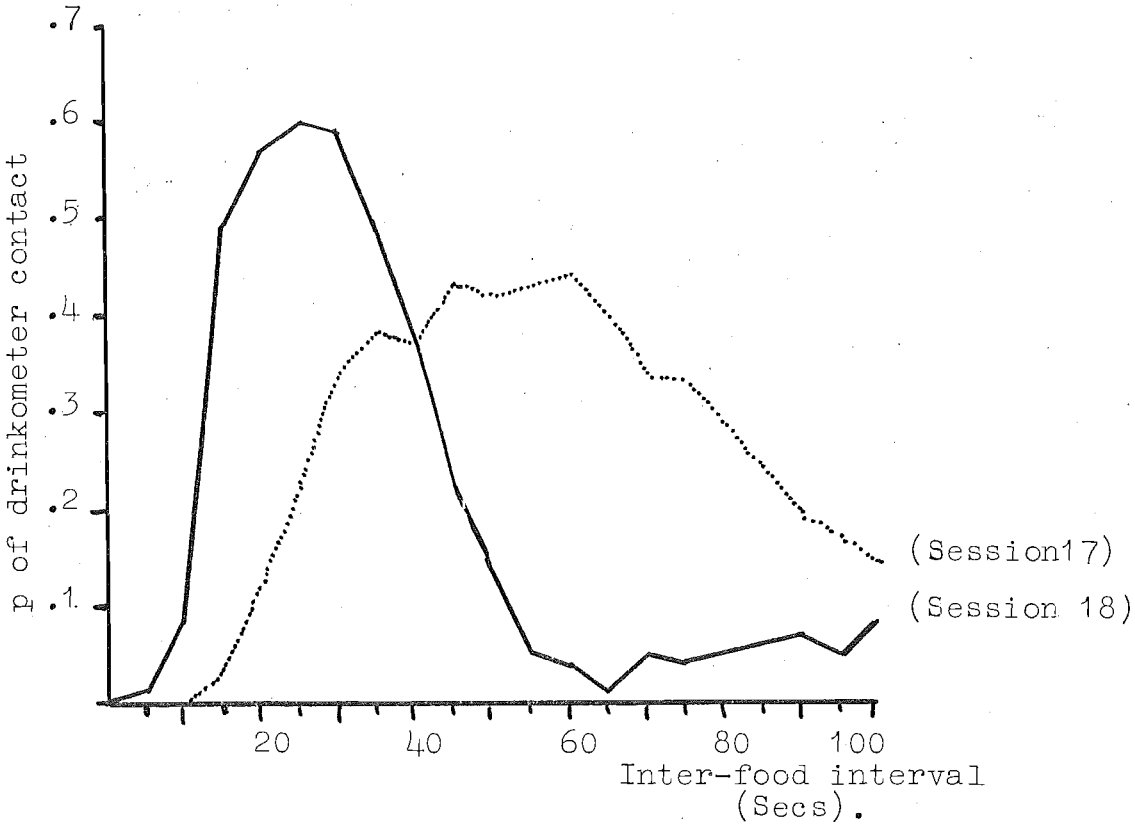
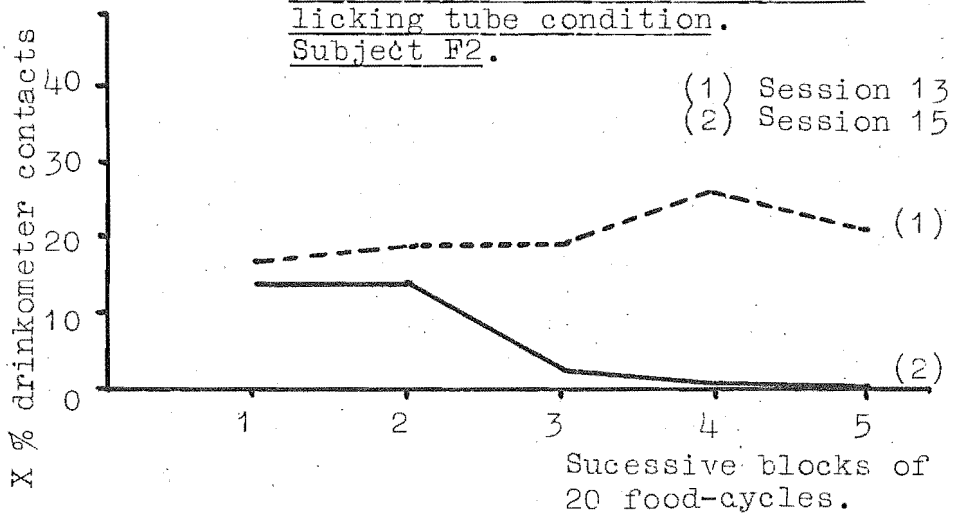
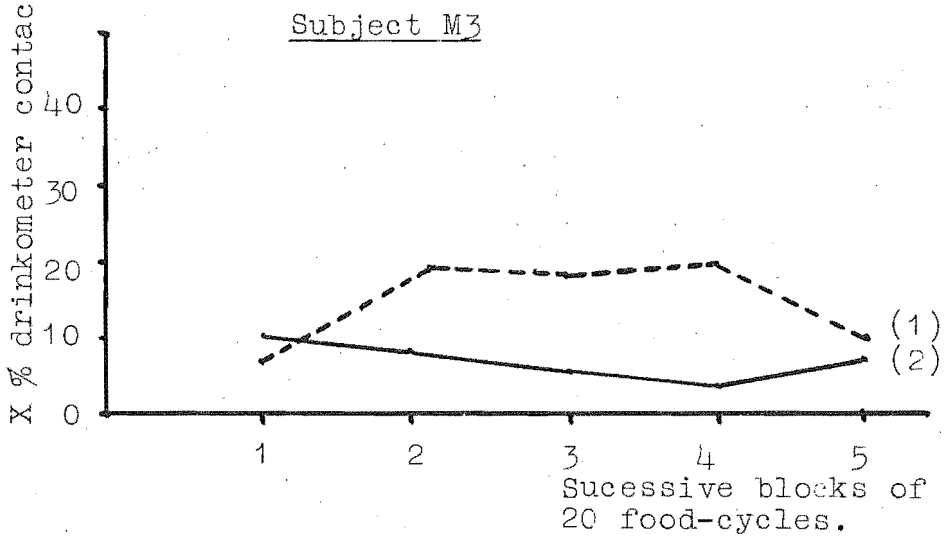


Figure 4:15 (a) Mean percentage drinkometer contacts per 20 cycles of food delivery licking tube condition.
Subject F2.



Subject M3



Subject M4

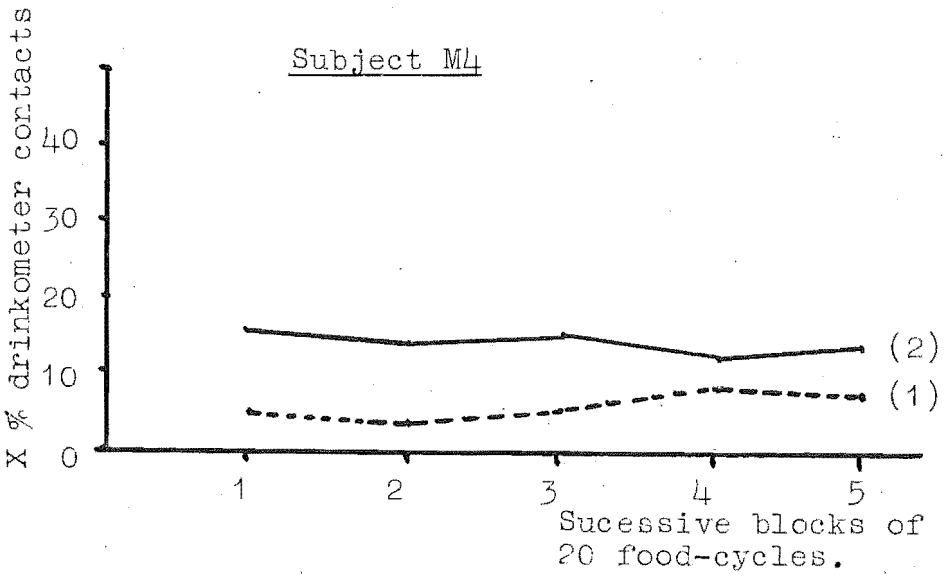
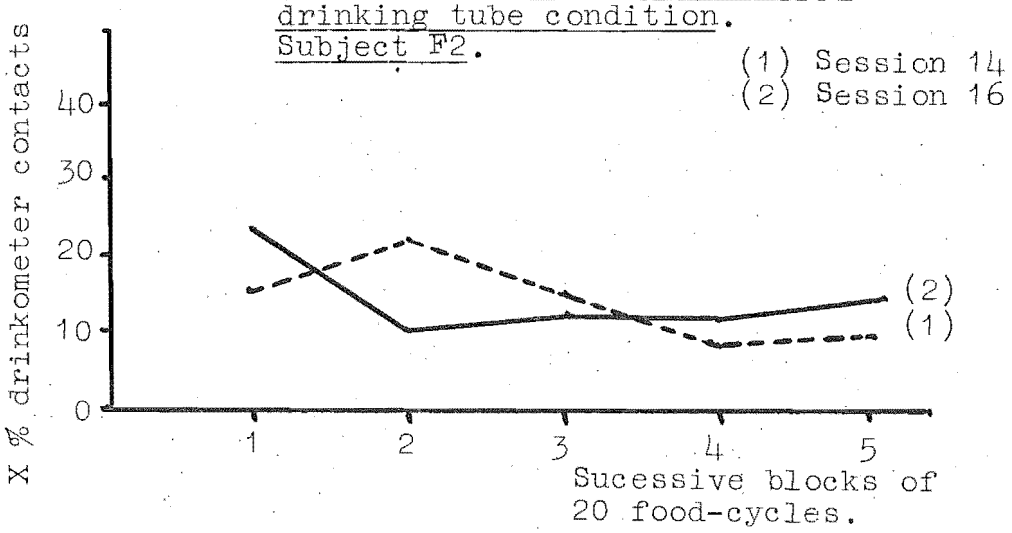
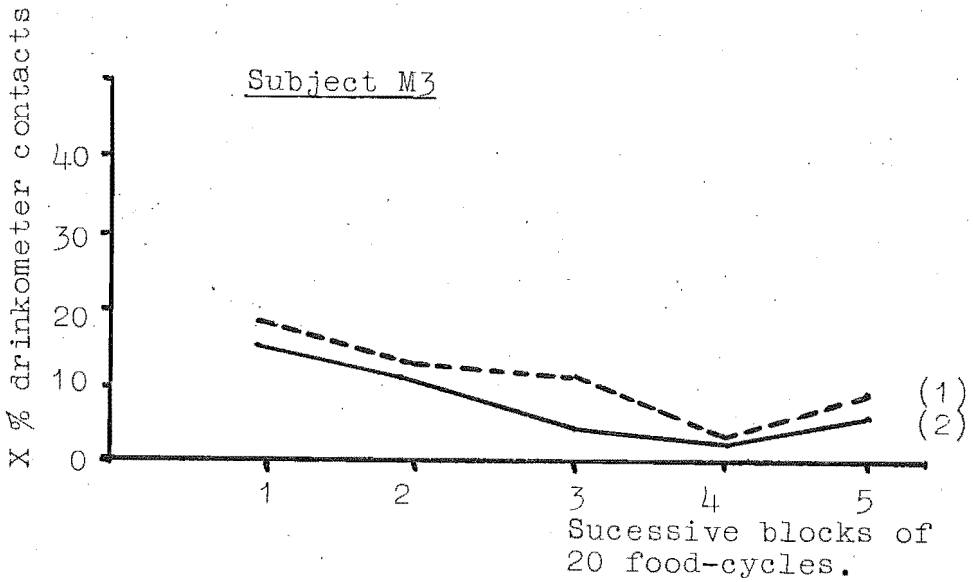


Figure 4:15 (b) Mean percentage drinkometer contacts per 20 cycles of food delivery drinking tube condition.

Subject F2.



Subject M3



Subject M4

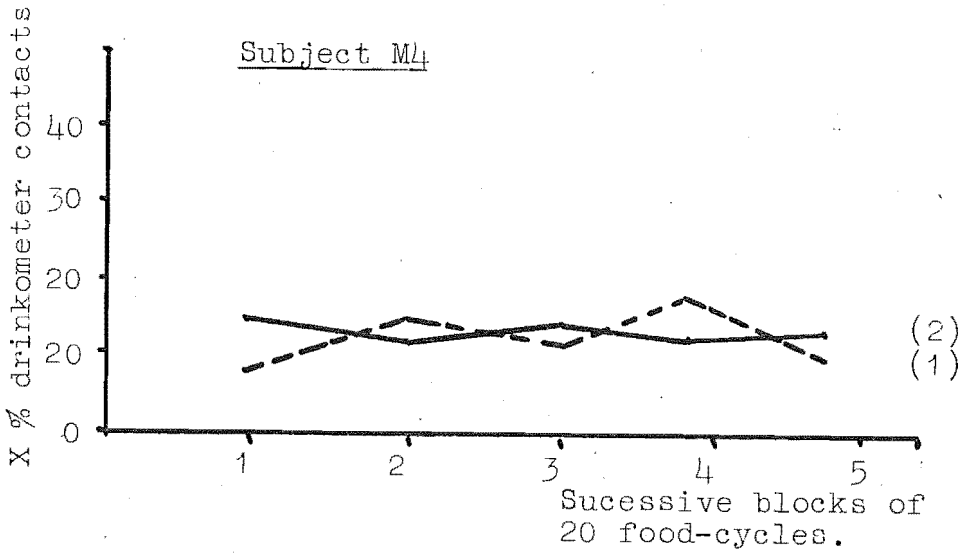
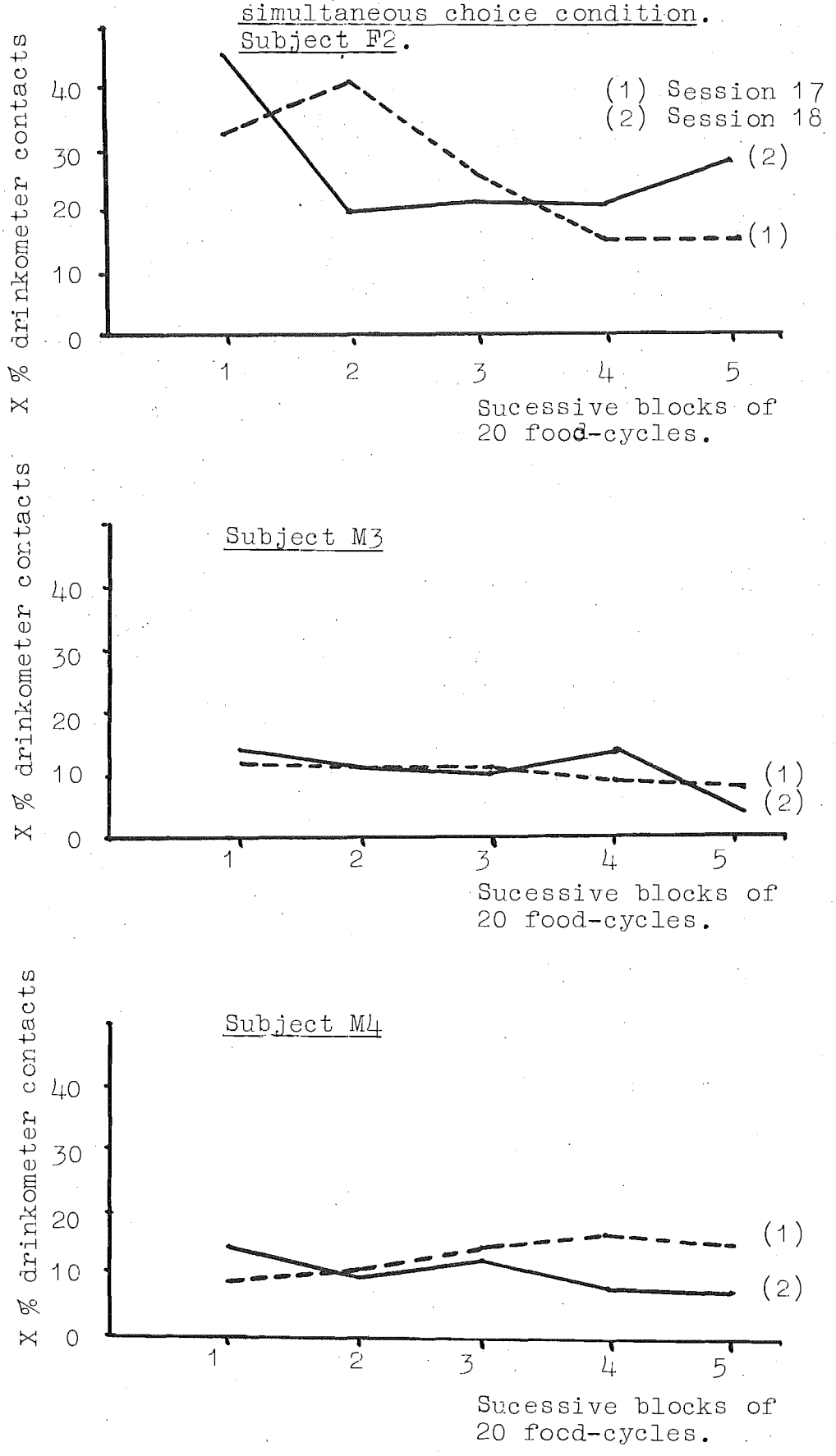


Figure 4:15 (c) Mean percentage drinkometer contacts per 20 cycles of food delivery simultaneous choice condition.



tube. This finding further emphasizes the role of individual differences under these experimental conditions, and reflects the behaviour of the pilot study subject.

(c) Control Sessions: The water intake levels recorded for each subject on sessions 19, 21 and 23 indicate that disconnecting the drinkometer does not affect schedule-induced polydipsia (as already noted by Falk, 1969). Observations of the subjects on sessions 20, 22 and 24 also confirm high levels of responding and although these conclusions are lacking in quantified evidence, they would also tend to support Falk's above mentioned findings. Due to the difficulty in obtaining quantified measurements of licking behaviour (in the absence of the drinkometer record) no absolute guarantee that the licking response is not under the control of drinkometer current effects is possible, but this prospect seems unlikely when the overall similarity of the two separate behaviours (i.e. drinking versus licking) are compared.

(d) Simultaneous Choice Situation: The data from all subjects indicate a clear preference for the drinking tube when a simultaneous choice was possible. As a result of this choice, all animals became polydipsic in the choice situations. This finding has an important bearing upon understanding of the licking tube responses, since they imply that the subject "elects" to develop polydipsia (with its attendant physiological stress).

(e) The Temporal Distribution of Drinkometer Contacts: The distributions obtained in this experiment reflect the individual differences that were observed in Experiment 2. However, the performances of the subjects in this study

on the licking tube are markedly different, as all subjects exhibited high levels of responding to this tube (unlike the attenuated responding observed in two of the subjects in Experiment 2). Generally the curves obtained from each subject are of a similar shape and magnitude irrespective of tube condition.

Individual differences between subjects appear to be expressed in responding late in the interfood interval, some subjects showed few responses in this area (eg. M3 and M4) whilst F2 showed a higher probability of responding up to the point of food delivery. All subjects again demonstrated a preponderance of responding in the early portions of the interfood interval, but these results still do not confirm an exclusive "immediate post-pellet" description for polydipsia.

The distributions of responding obtained in the simultaneous choice situation are similar to those from the drinking-tube-only and licking-tube-only conditions and indicate that the choice behaviour does not influence the results to any significant extent. This information lends support to the results showing a preference for *polydipsia over alternative behaviours*, and confirms the power of the inducing properties of this experimental situation.

The individual differences observed in these results emphasises the fact that schedule-induced polydipsia (and adjunctive licking behaviour) do not necessarily follow a rigid sequence (as compared with reflexive behaviour) but that a degree of flexibility exists in form and temporal locus as would be expected in a phenomenon that has its origins in a complex interaction between motivation-

al systems, morphology, and the environmental properties that provide a boundary condition to its expression.

The within sessions analysis showed a general decline in drinkometer contacts over the session length for the drinking tube condition (as was observed in the preceeding experiments) while the previously observed increase over the session of contacts with the licking tube was not evident (all subjects showed ambiguous results under this condition). Therefore it is not possible to generalise from these results as to whether the drinking tube provided satiation effects while the licking tube produced an increase in "thwarting" or "arousal" factors. This hypothesis is further discussed in the overview at the end of this chapter.

(f) General Discussion: The overall results from this experiment confirm the previously noted findings that generally the bulk of polydipsic responding occurs within the early portions of the interfood interval, but that sufficient responding occurs in the later portions of this interval to limit the application of the exclusive "immediate post-pellet phenomenon" description for this behaviour. Furthermore, the responding to the licking tube shows a similar pattern in this experiment.

The finding that subjects choose to respond to the drinking tube rather than the licking tube implies that the drinking response is more prepotent than the simple licking response, and indicates the existence of powerful motivational factors that govern this behaviour. These findings have a relevance to the role of phylogenetic factors in schedule-induced polydipsia.

A further important consideration relates to the high levels of responding recorded on the licking tube (in contrast to the results of the previous experiment) and indicates the existence of individual differences in behaviour towards this tube. Because of the individual variability observed, any generalisations about responding to the licking tube must of necessity be circumspect. Unlike responding to the licking tube, schedule-induced polydipsia was found to be a reliable and experimentally robust phenomenon from which generalisations can readily be made.

(E) An Overview.

The experimental paradigm used in this research has produced reliable levels of schedule-induced polydipsia in all subjects, and confirmed the robustness of this phenomenon. Although the levels of polydipsia obtained were not as high as some reported in the literature (200-300% as compared with 400-500%) the experimental water intake was still manifestly excessive, as can be determined by the depression of home-cage intake for up to 48 hours following polydipsic sessions. During the experimental sessions all subjects showed considerable physical durability, given the excessive physiological demands of this phenomenon, and only one subject (M2) showed a brief sign of ill-health as a possible consequence of excessive drinking. All animals were given limited exposure to the effects of excessive drinking on humanitarian grounds; although published reports indicate that rats have been

subjected to polydipsia over periods of several months.

The main intention of these experiments was to elucidate the temporal locus of the drinking, and to do this with the minimum of intervention with the recording techniques (i.e. to circumvent the use of levers, retractable tubes etc). The technique used produced reliable data as to where in the interfood interval drinking took place, and indicated that while the bulk of the drinking occurred early in the interval, some responding was possible throughout the latter portion up to the point of food delivery. These responses in the latter portions of the interval were most subject to individual differences, and this suggests that a different group of controlling factors might be involved. However, within the scope of the research goals of this study no test of this hypothesis was possible.

The existence of high levels of adjunctive licking (without water being consumed) was both an accidental and puzzling discovery. This particular behaviour was contrary to the reported findings from other research, and was more interesting because of the high levels of responding that were recorded from some subjects. Unlike schedule-induced polydipsia, there were wide individual differences in the degree of adjunctive licking, but most importantly where substantial levels of responding did occur, these followed a similar temporal distribution to polydipsia. Furthermore, unlike polydipsic responding which showed a decline over the session length (indicating satiation effects were operating) adjunctive licking tended to increase as the session progressed. There are several

implications from these results that may assist in the potential explanation for adjunctive behaviour.

First, two separate topographies may be involved; one being a drinking response, the other being a simple licking response. The experimental arrangement may influence both (although not to an equal degree) to produce similar forms of behaviour (i.e. as suggested by Segal, 1973).

Secondly, the adjunctive licking may be a form of schedule-induced tongue cooling (as reported by Mendelson and Chillag 1970) in which case two separate (though related) adjunctive behaviours exist in close behavioural proximity.

A third possibility relates to the adjunctive licking as being an unconsummated compontent of the drinking response, and is thereby under the same controlling factor as drinking, but owing to the absence of the consummatory feedback of liquid ingestion, continues to occur (and increase) because of the lack of a feedback control.

Finally, a number of minor factors may contribute to the behaviour (such as rewarding drinkometer current effects, "learned" licking of the tube, poor stimulus discrimination of the properties of the licking tube) but these appear unlikely, as the control sessions data indicate. However, these control data are not totally unequivocal, and would need further investigation to confirm this suggestion.

As these experiments examined the temporal aspects of polydipsia, it was not possible to investigate any of

these accounts for the existence of adjunctive licking. Accordingly, any accounts must remain conjectural, but one significant aspect remains from the choice experiment.

The finding that all subjects in the choice experiment "elected" to become polydipsic when a "less physiologically stressful" alternative was available emphasises the strength of schedule-induced polydipsia as a phenomenon. Whatever the explanation for adjunctive licking might be, the empirical findings that drinking to excess is the "preferred" behaviour emphasises the prepotency of this behaviour in this particular situation. The previously discussed issue regarding the adjustive ends served by polydipsia remains unanswered, but given the present choice data, it is apparent that some of the simple accounts that have been proposed for this phenomenon are not adequate Falk (1972) has considered the adjustive aspects that relate to adjunctive behaviour, and concludes:

> "If all behaviour is assumed to be either adjustive of pathological distortions of adjustment, by definition adjunctive behaviour must either be directly adjustive (which it seems not to be), serve an ancillary adjustive role (which has not been demonstrated and seems highly improbably), or be disordered adjustive reaction. This last would have to reduce to a functional disorder in that no pathological

> alterations have been instituted. While the neurotic may derive certain 'secondary gains' from his neurotic behaviour, the case for interpreting adjunctive behaviour in this regard is rather opaque. Nor does adjunctive behaviour seem to have the functional properties of neurotic behaviour. It develops rapidly rather than slowly, and it is characteristically predictable of all members of the species rather than idiosyncratic as to occurrence and form."

This latter point emphasises the fact that polydipsia appears to have a certain phylogenetic dimension that colours its expression. As was discussed in Chapter 2, the species-generality of schedule-induced polydipsia is a further dimension that contains questionable results and indicates the potential role of ecological factors. It is towards this issue that the next experiments are directed.

C H A P T E R F I V E

RESPONSES TO NON-CONTINGENT FOOD DELIVERY IN THE FERRET: AN ASPECT OF THE SPECIES-GENERALITY ISSUE.

(A) Introduction.

As was discussed in Chapter Two, the extent to which schedule-induced polydipsia has been demonstrated in species other than the rat has been a source of contention. Although this phenomenon is frequently described as occurring in pigeons (Shanab and Peterson, 1969), an attempt to replicate this study met with failure (Whalen and Wilkie, 1977). Not only did these researchers fail to obtain polydipsia in their subjects, but they also pointed out that Shanab and Peterson's results were based upon a solitary subject.

Similarly, Porter, Sozer and Moeschl (1977) claimed to have clearly demonstrated schedule-induced polydipsia in guinea pigs, although their results were largely based upon one subject (as two other subjects showed either little or no drinking). Furthermore, these authors acknowledged the findings of Freed, Zec and Mendelson (1977) who failed to find evidence of schedule-induced polydipsia in guinea pigs.

As well as there being a paucity of evidence demonstrating polydipsia in pigeons and guinea pigs, a failure to obtain this phenomenon in golden hamsters

has been reported by Wilson and Spencer (1975). These authors noted that most studies reporting schedule-induced polydipsia have used species that show a decrease in water intake when food deprived, and they were moved to comment that:

> "more comparative research is needed if the underlying determinants of schedule-induced polydipsia are to be discovered".

The lack of agreement as to the species-generality of adjunctive behaviour has been recognised by Falk (1977) who states:

> "The present evidence on species differences with regard to adjunctive behaviour is too fragmentary to enable the extraction of general principles".

The significance of determining the species-generality of adjunctive behaviour relates directly to the explanatory accounts for this phenomena. For example, Wayners' (1972) account of adjunctive behaviour, which is based upon lateral hypothalamic arousal mechanisms, might be considered as general account for this behaviour, as it presumably extends across a range of species. If a species-specific dimension is demonstrated, then modifications to this theory would be required.

Falk (1977) has considered the adaptive functions of adjunctive behaviour, and relates this aspect to a number of ecological factors that may be involved. In particular, he relates the mode by which a species exploits

food sources in its environment to its propensity to engage in adjunctive behaviours. He notes that some animals are highly mobile hunters (e.g. many carnivores and herbivorous seed and fruit eaters), and that this mobility is necessary since their food sources are "patchy" in availability. Other species are relatively less mobile (e.g. herbivorous grazers and browsers) since they are adapted to:

> "exploiting relatively small, densely supplied home ranges (McNab, 1963). Still other species move to a favourable place where, with immobile waiting, prey may be ambushed (e.g. bobcats, leopards, and many spiders and snakes)". (Falk, 1977)

Taking these differenes in mobility of foraging into account, he proposes that adjunctive behaviours serve an adaptive function of maintaining the animal in a situation whereby it might otherwise respond in a fugacious manner, i.e. attempt to move to another situation. He states:

> " The adjunctive behaviours block fugacity and keep the organism engaged with the situation - on the job".

From this basis Falk hypothesizes as to the propensity to engage in adjunctive behaviour in species of differing foraging modes.

> "It is possible that if adjunctive behaviour is, as suggested, a stabilizing activity maintaining the organism's engagement with a situation

> containing escape components,
> a minimally fugacious species
> may not require the diversi-
> fication of adjunctive behaviour
> to protect a nonoptimal, but
> feasible, feeding situation".

This refers to the browsing and grazing herbivorous species; whilst of carnivorous species he predicts:

> "..... the very mobile hunters
> with large prey-search times
> relative to prey-pursuit times
> (MacArthur, 1972, p61 ff), with
> rather low patch-fugacity thres-
> holds, *should yield food-schedule-*
> *induced adjunctive behaviour most*
> *readily*". (Italics mine)

This prediction bears specific reference to the carnivorous mode of existence, and may relate to the reported findings on one such species; the ferret. Pollard (1968) has observed that while ferrets perform well in the Yerkes Discrimination apparatus, and in the Hebb-Williams maze, they do not perform well in the operant bar-pressing situation. He has noted that while these animals could be trained to bar-press, they performed badly on schedules of reinforcement other than continuous-reinforcement (i.e. FR1 schedules). When alternate schedules of reinforcement were introduced, the ferrets developed "gambolling" behaviour, leading to long pauses between episodes of bar-pressing, with a consequent decrease in the number of reinforcements received. Pollard concluded that:

"The evidence suggests that unless
food can be obtained rapidly, at
least in the early stages of training,
large numbers of competing responses
are to be expected from this species".

The competing behaviour in this instance was not related to bar-pressing behaviour, but directed away from the food-hopper, where the subjects engaged in a number of activities that prevented their returning to feed (Pollard, 1973, personal communication). As this species exhibits such activities when food deprived, it was conjectured that they might also develop adjunctive behaviours in a response non-contingent situation. Accordingly, ferrets were placed in an analogous experimental situation to that known to produce schedule-induced behaviour in rats, in order to test this hypothesis.

Two adjunctive behaviours were selected for investigation; these being schedule-induced polydipsia and schedule-induced wheel-running. Polydipsia was selected to further examine the species-generality of this phenomenon *apropos* the issues previously discussed. Schedule-induced wheel-running was selected because it is well demonstrated in rats (e.g. Levitsky, 1967; Levitsky and Collier, 1968; Segal, 1969), is ammenable to automatic recording techniques, and is an "activity" related behaviour. This latter point bears reference to what Breland and Breland (1966) call "cheap" behaviour. In discussing the behaviour of the porpoise they observe:

"It is important to realise that the
behaviour of the porpoise is very "cheap".

> Activity comes readily and easily and at low cost in terms of risk and organismic committment". (p86).

They further point out that in designing experimental situations for porpoises and

> "other quick-moving "cheap behaviour" animals, it is important in the first place to make the behaviour sufficiently difficult so that it "means something" to the animal".

This concept of "cheap" behaviour has relevance to the behaviour of ferrets, since this species is known to engage in highly active behaviours in the experimental situation (the "gambolling" behaviour as described by Pollard, 1968).

As was discussed in Chapter 3, a further justification for using the ferret as an experimental subject related to the ongoing research programme with this species within the Department in which these studies were conducted.

The experimental paradigm used to investigate the behaviour of ferrets was identical to that used in studying schedule-induced polydipsia in the rat. The only differences related to the experimental chamber used, and the type of food provided.

Experiment 1: Attempts to obtain Schedule-Induced Polydipsia in the Ferret.

Subjects:

2 male and 2 female experimentally naive ferrets aged approximately 310 days served. The subjects respectively weighed 1325 grams (M1), 1550 grams (M2), 800 grams (F1), and 950 grams (F2).

Apparatus:

A similar experimental situation was used, as in the rat-studies (Chapter 4), with a larger experimental chamber substituted. Details of the Ferret Chamber are given in Appendix 3. The food comprised small pieces of fresh meat (weighing approximately 1.0 - 1.5 grams) which were dipped in cod-liver oil to facilitate their use in the automatic feeder.

Procedure:

The individual daily home-cage water intake was recorded for 7 days prior to the subjects being food deprived to 90% free-feeding weight. The subjects were then maintained at 90% free-feeding weight by feeding once every 24 hours. Home-cage daily water intake was again recorded for 7 days. The subjects were then given 30 minute habituation sessions in the experiment setting, over 3 successive days, with oil-covered meat portions being freely available in the food receptacle.

There followed 18 daily sessions, in which the subjects received 100 food-portions on a FF1 100 second schedule of delivery, with water continuously available from a drinking spout that was connected to a drinkometer. White noise was present during all sessions. Home cage water was available continuously, and daily intake was

monitored for each animal.

Results:

(a) Water Intake: The home cage daily intake at 100% and at 90% free-feeding weight are presented in Table 5.1. This indicates no appreciable changes in the level of intake with food deprivation. The daily water intake over the experimental sessions is given in Table 5.2, and again indicates no change in the level of intake.

(b) Number of Licks: These are presented in Table 5.3, and reveal a low level of responding in a sporadic pattern.

(c) Uptake of Food: The subjects consumed all the meat portions within the experimental session, as a post-session examination of the chamber revealed no evidence of hoarding. Observation of the subjects during the session revealed that they often did not take a piece of food immediately after it was delivered, but engaged in gambolling about the door, returning to take several pieces of meat at a later time.

Discussion:

The results indicated that there was no evidence of schedule-induced polydipsia in these subjects, but a number of methodological considerations may have accounted for these findings. Firstly, the subjects may have been insufficiently food deprived. Secondly, the meat portions may have contained sufficient fluid to depress drinking behaviour to the low level recorded. Thirdly, schedule-induced polydipsia may take longer to develop in the

Table 5.1: Daily Water Intake (mls).

Condition	Day	M1	M2	F1	F2
100% Free-	1	54	60	38	22
Feeding	2	49	52	19	26
Weight	3	30	47	28	30
	4	16	26	8	33
	5	37	48	24	16
	6	31	21	19	17
	7	39	23	28	16
Mean		36.5	39.5	23.4	22.8
90% Free-	1	41	28	14	27
Feeding	2	27	33	23	21
Weight	3	32	43	21	29
	4	38	49	34	19
	5	26	42	26	29
	6	35	41	18	20
	7	40	39	17	34
Mean		34.1	39.3	21.8	25.5

Table 5.2: Experimental Session Water Intake (mls).

Session	M1	M2	F1	F2
1	0.3	0.0	0.0	0.9
2	0.0	0.0	1.7	0.3
3	1.4	3.1	0.0	0.0
4	0.1	0.0	0.5	0.0
5	0.0	1.1	0.0	0.0
6	0.0	4.1	0.0	0.0
7	0.0	0.1	0.0	0.0
8	2.3	0.0	2.1	0.0
9	0.0	0.0	4.2	0.0
10	0.0	0.0	0.0	0.0
11	0.0	0.0	0.7	0.0
12	0.0	0.0	0.0	0.0
13	0.9	0.8	0.0	0.0
14	0.0	0.0	0.0	0.0
15	0.0	6.1	0.0	0.0
16	0.0	0.0	0.6	0.0
17	0.4	0.9	0.0	0.0
18	0.0	0.0	0.3	0.0

Table 5.3: Number of Licks.

Session	M1	M2	F1	F2
1	47	0	0	108
2	0	0	147	31
3	203	391	0	0
4	11	0	57	0
5	0	118	0	0
6	0	432	0	0
7	0	21	0	0
8	364	0	281	0
9	0	0	518	0
10	0	0	0	0
11	0	0	86	0
12	0	0	0	0
13	122	140	0	0
14	0	0	0	0
15	0	615	0	0
16	0	0	83	0
17	76	77	0	0
18	0	0	34	0

ferret than in the rat. This latter possibility seems unlikely, but could be tested by further exposing the subjects to the experimental situation. The meat portions were found to be unsatisfactory, since it was difficult to control for portion size, and the cod-liver oil was found to cause an undesirable stickiness in the delivery tube. Thus the food was changed to "Dog Sausage" (see Appendix 4 for details) as this was less moist, of constant density, and was easy to cut into equal sized pieces (of about 1 gram weight).

With the food changed to this latter type, and with the subjects having had 18 sessions exposure to the experimental situation, a repeated experiment was conducted, with the subjects being further food deprived to 85% free-feeding weight, in order to encourage the potential development of schedule-induced polydipsia.

Experiment 2: A Replication at a Greater Level of Deprivation.

Apart from the greater level of food deprivation and the different food, this experiment was identical to Experiment 1.

Results:

After 18 sessions both the water intake and the number of licks still remained at the same level as in Experiment 1 - see Tables 5.4 and 5.5. An observation of the subjects indicated that they still occasionally persisted in gambolling about the door instead of going to the food receptacle to eat, but this behaviour was

Table 5.4: Experimental Session Water Intake (mls)

Session	M1	M2	F1	F2
1	0.0	1.9	0.8	0.0
2	0.0	1.2	0.0	0.0
3	1.7	0.0	0.2	1.2
4	0.5	0.0	4.3	0.2
5	0.0	0.0	0.0	0.0
6	0.4	0.0	1.8	0.0
7	0.0	0.7	0.3	0.0
8	0.0	0.0	0.0	0.7
9	0.0	0.8	0.0	0.0
10	0.0	0.8	0.0	0.0
11	2.9	0.1	0.0	0.3
12	0.0	0.0	0.6	0.0
13	0.0	0.0	0.0	1.3
14	0.6	0.0	0.0	0.0
15	0.0	0.0	2.0	0.0
16	0.1	0.3	0.0	0.0
17	0.0	0.9	0.0	0.1
18	0.0	0.0	0.0	0.5

Table 5.5: Number of Licks.

Session	M1	M2	F1	F2
1	0	168	88	0
2	0	96	0	0
3	249	0	39	120
4	62	0	599	12
5	0	0	0	0
6	47	0	152	0
7	0	93	44	0
8	0	0	0	71
9	0	80	0	0
10	0	97	0	0
11	394	7	0	32
12	0	0	95	0
13	0	0	0	163
14	89	0	0	0
15	0	0	203	4
16	18	29	0	0
17	0	128	0	6
18	0	0	0	59

less frequently observed than when fresh meat portions was used.

Discussion:

Once again the results indicated that no schedule-induced polydipsia developed in these subjects. However, another methodological criticism would be levelled at the possibility that the water-spout may not have had sufficient discriminative properties for the subjects to direct sustained behaviour towards it. Although some licks were recorded, these were always sporadic in occurence, and less than 1 ml of water was consumed in any session. Accordingly, if water was substituted with another more preferable liquid (e.g. milk) then this may serve to sensitize the subjects to the tube. Laboratory experience had demonstrated that ferrets showed a preference for milk which they drank avidly, and this would provide a suitable substitute liquid to sensitize drinking behaviour.

Experiment 3: The Effects of Substituting Milk for Water.

Apart from the substitution of milk for water on the first 7 sessions, this experiment was a repetition of the previous two studies with the subjects maintained at 85% free-feeding weight. After receiving milk on the first 7 sessions the subjects then received water for the remaining 11 sessions.

Results:

(a) Milk Intake: The data on milk intake are given in Table 5.6, and indicate a high level of consumption,

Table 5.6: Experimental Session Milk Intake (mls).

Session	M1	M2	F1	F2
1	204	176	54	42
2	248	160	46	36
3	174	156	84	36
4	360	344	186	78
5	190	130	58	86
6	396	132	38	43
7	201	184	92	59

Table 5.7: Number of Licks.

Session	M1	M2	F1	F2
1	4731	2094	1816	1494
2	5390	1847	1692	1182
3	3944	1716	3269	1247
4	7831	6284	4619	2693
5	4292	1392	2144	3298
6	8943	1499	996	1674
7	4557	2684	3727	2386

compared to the daily water intake. The number of licks recorded also reflects this high level of contacts with the drinking-tube, as Table 5.7 reflects.

Observation of the subjects revealed that they were satiated on milk early in the experimental session, and consequently did not eat all the food portions that were subsequently delivered. The numbers of pieces of food not consumed at the end of the session are given in Table 5.8. Despite the amount of milk consumed there was no evidence of overhydration (i.e. quantities of urine) as in the case with polydipsic rats.

(b) Water Intake: Immediately after a reversion to water in place of milk the subjects indicated a similar pattern of no contact with the water tube (as was observed in the first two experiments), see Tables 5.9 and 5.10.

Discussion:

The results clearly indicate that the subjects more readily consumed high levels of milk on the days when this was present in the experimental situation. These data also indicate the potential levels of liquid intake in these animals under conditions of high palatability; levels which were not obtained with water in this experimental situation. Despite a total of 47 sessions each of 166 minutes duration (discounting 7 sessions in which milk was available) no evidence was found of schedule-induced polydipsia in the sample of ferrets used. Contacts with the drinking tube were of a sporadic nature, with insignificant levels of water being consumed. Homecage water intake levels over this period remained

Table 5.8: Number of Food Portions Unconsumed.

Session	M1	M2	F1	F2
1	42	29	45	21
2	57	37	37	30
3	38	18	53	44
4	49	61	76	52
5	41	48	34	49
6	65	67	31	41
7	43	31	43	33

Table 5.9: Experimental Session Water Intake (mls).

Session	M1	M2	F1	F2
8	0.1	0.0	1.3	0.7
9	0.0	0.0	0.6	0.2
10	1.4	0.0	0.0	0.0
11	3.8	1.5	0.8	0.0
12	0.3	0.0	0.6	4.8
13	0.0	0.7	0.1	3.4
14	0.0	0.9	0.0	1.1
15	0.6	0.6	0.0	0.6
16	0.0	0.0	2.6	0.0
17	0.0	0.4	0.0	1.2
18	0.0	0.0	1.4	0.0

Table 5.10: Number of Licks.

Session	M1	M2	F1	F2
8	18	0	161	52
9	0	0	74	27
10	126	0	0	0
11	262	214	104	0
12	66	0	81	413
13	0	130	10	291
14	0	173	0	184
15	143	126	6	47
16	0	0	309	0
17	0	84	0	226
18	0	0	178	0

relatively unaffected by this experimental manipulation (unlike those of rats where significant decrease in home-cage intake occurred following polydipsic sessions). It is concluded that the procedure which produces shcedule-induced polydipsia in rats does not produce similar behaviour in food-deprived ferrets. Hence it appears that a boundary condition to schedule-induced polydipsia is involved, regarding the species-generality of this behaviour (as has been demonstrated with at least one other species: the golden hamster). However, these results do not discount the possibility of other adjunctive behaviours being demonstrated with this species.

Experiment 4: Attempts to obtain Schedule-Induced Wheel-Running in the Ferret.

Subjects:

The same subjects as used in the previous three experiments served. They were maintained at 85% free-feeding weight, as they did not appear to suffer any deleterious effects upon their health at this level; a level that should maximise the development of potential schedule-induced behaviours (as compared with 90% free-feeding weight).

Apparatus:

The same experimental chamber was used as in the previous studies with the addition of a suitably sized activity wheel. The details of this wheel are given in Appendix 3.

The design of this activity wheel was strongly influenced by the behaviour of the subjects, since a number of mishaps befell it until modifications made it "ferret-proof" (i.e. relatively indestructible). Initially the subjects used the flexibility of the diamond-mesh near the top of the wheel to assist in their escaping out into the research room. When this was remedied they then succeeded in fracturing the welding around the axle and the hub through the torsional-stress induced by their changing direction whilst the wheel was in motion. With the axle and hub suitably strengthened to prevent future facture of this welding, a subject then pulled the gauze mesh that formed a "floor" of the activity wheel into the main experimental chamber, thereby jamming the activity wheel in place. With this repaired, the wheel was found to be reliable and strong, despite the necessity for a lightweight design (dictated by fact that a sturdy heavy structure would possess excessive inertia, and would thereby prove impractical for the ferrets to stop it readily). The degree of "destructive ingenuity" exhibited by the ferrets in these early stages confirmed their suitability as subjects for an experiment examining high activity levels of behaviour.

Procedure:

Having rectified difficulties with the activity wheel the subjects were then given daily sessions in the apparatus, during which time they received 50 pieces of meat on a FF1 100-sec schedule. Thus the session length was 83.3 minutes. In all, each subject received 21 sessions in this situation. The number of revolutions,

and the frequency of food delivery were recorded on an Esterline-Angus event recorder (with a secondary record of revolutions being provided on a separate counter also).

Results:

The data on the number of wheel-revolutions per session are given in Table 5.11, and parallel the results from the earlier experiments, in that they show a low level of responding of a sporadic nature.

Discussion:

The results indicate a failure to demonstrate schedule-induced wheel-running in ferrets. Like the attempts to obtain schedule-induced polydipsia in these animals, an experimental manipulation that has been shown to produce increased wheel-running in rats apparently does not produce the same effects in ferrets. These results have a significance for any account for schedule-induced phenomena, as they imply limitations upon the species-generality of such adjunctive behaviours. While it would be premature to discount the possible existence of schedule-induced behaviours in ferrets, the present results indicate that at least two commonly obtained adjunctive behaviours in rats do not readily occur in ferrets. Any explanation for this discontinuity would necessarily be speculative. It is of interest to note these data do not support Falk's prediction regarding the propensity to engage in adjunctive behaviour in the carnivores (see page 5:4), although this is further considered in Chapter 7. However, there remains a methodological problem that does have some bearing on these

Table 5.11: Number of Wheel Revolutions per Session.

Session	M1	M2	F1	F2
1	178	29	14	476
2	361	97	11	615
3	204	582	0	118
4	18	133	3	0
5	2	0	0	0
6	0	0	0	96
7	14	64	0	0
8	0	17	0	0
9	38	4	0	28
10	106	5	7	47
11	11	0	0	31
12	0	32	38	0
13	0	106	0	21
14	4	0	0	6
15	71	0	0	0
16	0	3	8	0
17	29	0	0	0
18	2	0	2	18
19	18	35	0	3
20	0	2	0	0
21	41	0	0	5

results, and relates to the nature of the laboratory method by which schedule-induced behaviours are investigated. One of the prime reasons for selecting drinking and wheel-running as schedule-induced behaviours to investigate in the ferret (apart from the fact that they are well demonstrated in rats) is the ammenability of such behaviours to automatic recording. Despite the obvious benefits of automatic recording the experimenter is still ignorant to the larger extent, as to what behaviours the subject may be engaging in from moment to moment, and consequently much valuable information may be lost as a result of this prescription for automatic recording. It is to this question that the research in the next Chapter is directed, since a comparative analysis of what the two species do in an analogous situation may provide some clarification of the results obtained.

C H A P T E R S I X .

RESPONSES TO NON-CONTINGENT FOOD DELIVERY:

A COMPARATIVE OBSERVATIONAL ANALYSIS.

(A) Introduction.

(B) General Experimental Rationale.

- (1) Frequency of observation.
- (2) Choice of behaviour categories.
- (3) Method of analysis.
- (4) The behaviours studied.

(C) The Categories of Observed Behaviour.

- (1) An attempt to standardise categories.
- (2) The categories of behaviour: Rats.
- (3) The categories of behaviour: Ferrets.
- (4) A summary of the overall categories: the organism-information approach.

(D) A Comparative Observational Experiment.

Subjects
Apparatus
Procedure
Results
- (1) The method of analysis.
- (2) The rat experiment.
  - results.
  - discussion.
- (3) The ferret experiment.
  - results.
  - discussion.

(E) General Discussion.

C H A P T E R S I X

RESPONSES TO NON-CONTINGENT FOOD DELIVERY: A COMPARATIVE OBSERVATIONAL ANALYSIS.

(A) Introduction.

In discussing their experiences with a variety of animals over an eighteen year span, Breland and Breland (1966) made the following comment about the value of observational methods in their research:

> "Thus, we feel the observations are of considerable value in the understanding of animal behaviour in general and that our interpretive hunches stand generally on pretty firm ground. It has been largely this observational material, plus the considerable background reading we found necessary in order to make sense out of the behaviour of our animals, that led us to the naturalistic evolutionary theoretical look at behaviour which we have just presented". (p. 71)

This statement bears signal reference to an issue arising out of the experiments which have been described in Chapters 4 and 5; for although the results have

elucidated the temporal locus of schedule-induced polydipsia in rats, and have indicated that this behaviour does not readily develop in ferrets, there still remains an unanswered question as to what other behaviours occur in the experimental situation?

The benefits that are bestowed by the use of automated recording instruments are readily apparent, since accurate and consistent data can be recorded over long periods, with a consequential gain when analysis of the data is attempted. However, beyond the measures of behaviour obtained from drinkometer contacts, activity-wheel revolutions, and amounts of water consumed, there exists an array of behaviours that are unrecorded, and unobserved. An implicit problem with automation of data recording is that other sources of potentially valuable information are disregarded.

With respect to the experiments described in the previous two chapters, a number of questions are raised appertaining to the differing behaviours of rats and ferrets. Firstly, there is the question of what behaviours change in frequency when the rats develop polydipsia, since this phenomenon progressively increases in magnitude until it reaches asymptote. Secondly, with regard to the ferrets, a question arises as to what behaviours occur between successive food deliveries, and whether these behaviours reveal any temporal patterning. A third consideration, again applying to the ferrets, is whether there are any defined patterns of behaviour that may be ammenable to investigation through the design of appropriate equipment (e.g. do ferrets engage in

scratching behaviour that may be investigated through the provision of a small tread-mill etc.?)

These questions may be answered, in part, by observing the behaviour of these species using a time-sampling procedure. Furthermore, this approach provides an opportunity to apply to these two species the comparative method of analysis discussed in Appendix One.

(B) General Experimental Rationale.

The use of observational time-sampling measures of behaviour is a technique that has been commonly applied to the study of exploratory behaviour and responses to novelty (e.g. Bindra and Blond, 1958; Bindra and Spinner, 1958; Woods, 1962). This technique has also been applied to an assessment of the effects of septal and frontal ablations in rats (Lubar, Herrmann, Moore and Shouse; 1973), and to aspects of avoidance responding in rats (Baum, 1970).

Important features of the time sampling technique relate to the frequency of observation, the choice of behaviour categories to be described, and the method of analysing the data. These are considered separately below.

(1) Frequency of Observation.

The frequency with which observation occurs is a significant determinant of the quality of data obtained. Clearly, if behaviour is sampled every second, it will provide a more comprehensive description of what the subject is doing than if it were sampled every 30 seconds.

These considerations are reviewed by Delius (1969), Andersson (1974) and Altmann (1974).

In general, the more frequent the time sample is taken, the more accurate the description of the behavioural events becomes. In the case of the research described in this chapter, a time-sample was taken every two seconds, providing a data-base of fifty observations per cycle of food delivery.

(2) Choice of behaviour categories.

An important aspect of the choice of behaviour categories is that they be descriptive as far as possible, rather than interpretive. (Bindra and Blond, 1958). Also the categories chosen need to be mutually exclusive, allowing only one category to be recorded on any given observation. Bindra and Blond comment on the necessity to adopt an order of priority system when two categories occur simultaneously, so that only one category is scored; in practice this was found to be necessary, athough the behaviour categories adopted were found to be readily classifiable in most instances. A further suggestion that Bindra and Blond found important relates to the need to make the categories exhaustive, thus the necessity for a 'miscellaneous category (covering those behaviours that occur infrequently).

(3) Method of analysis.

As there were several categories of behaviour some method of simplifying these categories for purposes of analysis was deemed necessary. This related to the fact

that several categories of behaviour were "collapsible" (i.e. two or three categories could be combined because of their overall similarity to make up one overall category). An example of collapsing categories can be taken from the overall category *immediate food-oriented behaviours* which was comprised of the observed categories of "Eating" and "Head in food hopper". [1]

Also, as the various categories were recorded over a regular time cycle, it was possible to derive temporal distributions for each category of behaviour. However, it was necessary to use only the "collapsed" overall categories in order to simplify the presentation of the temporal distributions for each experimental subject.

(4) The behaviours studied.

An observational analysis of the behaviour of rats and ferrets in this experimental situation gives rise to an array of empirical questions, and therefore it was felt necessary to impose restrictions upon the experimental goals of the study. Consequently, it was decided to concentrate solely upon schedule-induced polydipsia in the rats, and to ignore other potentially interesting phenomena such as schedule-induced wheel-running and schedule-induced responding to the licking-tube. This latter behaviour was excluded from the analysis because it was an unexpected discovery that was not fully understood in terms of causation and properties (although

1. To avoid confusion between the general categories of behaviour and the overall "collapsed" categories, the latter are always presented in italics.

it is a subject worthy of more extensive examination).

Thus the goal of this experiment was to examine the changes in the various observed behaviours in rats as schedule-induced polydipsia developed, and to compare these data with the behaviour of ferrets in an analogous situation. It was anticipated that the experimental data would help to explain why polydipsia did not develop in ferrets. Also, this would indicate potential behaviours that may be suited to some future experimental manipulation in this species.

(C) The Categories of Observed Behaviour.

The categorisation of behaviour was relatively easy in the case of the rat experiments, as precedents existed in the work of Bindra and Blond, and Bindra and Spinner. However, the ferrets provided a more difficult problem as no pre-existing categories were available for this species. Consequently a brief pilot study was undertaken with a surplus naive subject, in which the animal was observed and its behaviour categorised in a similar manner to that of the rat. These categories were found to be satisfactory in the subsequent experimental study.

(1) An attempt to standardise categories.

In order that some standardisation of the categories be achieved, each category is described below, with the rules for applying priority of recording whenever this was appropriate. Furthermore, most behaviours are shown photographically at the end of this section. The

photographs give some indication of the topography of the respective behaviours; but naturally some behaviours are difficult to show by this method.

The rapid and unpredictable movements of the subjects made photography difficult. To minimise movement effects, a high shutter speed was used (1/500th sec.) with a high speed film (Kodak 400 X, ASA 400/Din 27, at an aperture setting of $f/1^4$ to $f/2^2$). At these settings the lighting was still not ideal for photography, given the rapid movements of the subjects across the experimental chambers. Accordingly, some categories did not photograph well and have been left out. An additional problem related to the distractibility of the subjects, who tended to engage in a limited repetoire of behaviours in the presence of the photographer. Consequently, the rats often remained stationary for long periods or approached the door and sniffed the small gap at the bottom. The ferrets tended to engage in protracted bouts of scrabbling at the door, and rarely exhibited the appropriate behaviours to be photographed. The photographic sessions occurred two days after the final experimental observational session (i.e. day 17).

(2) <u>The categories of behaviour: Rats</u>.

(a) Head in the food receptacle: (H). This category included all those occasions when the subject had its head in the food receptacle. The receptacle was transparent, providing a reasonable view of the subject (although it was sometimes difficult to ascertain what behaviours were occurring in the receptacle when the

subject had its back to the viewing position). Other behaviours that occurred simultaneously while the subject's head was in the hopper included eating, and sniffing. However, a priority rule was applied in this instance (as noted in Bindra and Blind), so that H became the recorded category. As expected, this behaviour tended to occur in the immediate interval following food delivery (where it often recorded an occurrence of 100%) with few instances being recorded later in the interfood interval. See Plate R 1.

(b) Eating: (E). Although the rats often commenced eating in the food receptacle (i.e. in category H), they frequently removed the food pellets to the outside of the receptacle to consume. Thus E followed H in most instances. Because of this close relationship categories E and H were "collapsed" in the data analysis to provide an overall category entitled *immediate food-oriented behaviours* in deference to the role of the food receptacle, this overall category being shown as category 1 in the analysis. See Plate R 1.

(c) Ambulation: (A). This category describes the general ambulatory movements of the rat, whether it be walking or running. It differs from other locomotor categories in that it involves the animal changing its spatial location within the horizontal plane of the experimental chamber. This category was classified as locomotion by Bindra and Blond. The major problem encountered with this category related to the category S (sniffing), since the animal frequently exhibited the characteristics of sniffing behaviour while it was moving. In these situations a priority rule was

applied, in which A took precedence over S, unless the animal was actually in close physical proximity (i.e. approximately 5 cms or less) to an object (towards which the animals head was oriented, and the animal was sniffing). See Plate R 2.

(d) Sniffing: (S). This behaviour entailed rapid movements of the vibrissae, usually with nose-twitching and a directed head-orienting response. Bindra and Blond note that "sound of sniffing" is another characteristic of this behaviour, but with white-noise present this was inaudible. As mentioned in the case of ambulation, sniffing took a lower priority when the subject was engaged in general movement; however it would be unreasonable to assume that sniffing did not occur on these occasions to some degree. This situation is a good example of the need for a priority rule in observational experimental situations. See Plate R 3.

(e) Rearing: (R). The rearing behaviour consisted of the subject raising its front paws off the floor, and arching its back upwards along the vertical plane. Bindra and Blond classified this behaviour as an example of sniffing, but since a clearly defined postural change occurs (involving an overt change in vertical orientation) it was scored as a separate category. Rearing was also included touching the walls of the chamber when standing upright. See Plate R 4.

The categories A, S, and R were grouped together under the overall (collapsed) category of *active investigatory behaviours* (being shown as category 2 in the analysis). This grouping was based upon the assumption that such behaviours

involve "active information seeking" about the immediate environment, and is an assumption that is derived from the "organism-information approach" as discussed by Garcia, Clarke and Hankins (1973). Details of this approach are further elaborated in sub-section 4 of this section of the chapter.

(f) Drinking: (D). Drinking was defined as responses directed at the drinking tube, and was unique in that it was more objective than the other categories because of the independent verification of this behaviour through the drinkometer recordings. Strictly, this category defines licking behaviour, but as the rats developed polydipsia within a few sessions it was classified as drinking. As the goals of this study were directed at investigating schedule-induced polydipsia, this category was not "collapsed" but remained separate as category 3 in the analysis. See Plate R 5.

(g) Grooming: (G). Grooming behaviour was described as the licking, scratching, and preening of any part of the body, and also "nibbling" of the tail while this appendage was held in the forepaws. This behaviour was directed towards the animals body, with little or no activity overtly directed at the rest of the immediate environment, while the animal was engaged in grooming.

Since the rats engaged in this behaviour to some magnitude, and did not move about the experimental environment while engaging in grooming, it was classified as a form of *stationary behaviour*. This label applies only to the fact that the subjects were not engaged in active locomotory activity, as obviously they were not sitting

still while grooming. See Plates R 6 and R 7.

(h) Stationary: (F). This category was defined as sitting motionless, in a hunched or prone position, with occasional trembling of the body, and with the eyes open. This category is sometimes termed "freezing" (e.g. Bindra and Blond) but the term stationary is preferred here since it is less interpretive. See Plate R 8.

As with category G (grooming) the subjects were not engaged in any overt locomotory activities, and accordingly F and G were "collapsed" into the overall category of *stationary behaviours*, appearing as overall category 4 in the analysis. As with the overall category 2 (*active investigatory behaviours*) category 4 also falls into the schema of the organism-information approach.

(i) Miscellaneous (M). This category was adopted to make the categories jointly exhaustive, and provided a means of identifying several low probability behaviours. These included defecation, urination, gnawing of the floor, pica, and climbing up the inside of the food hopper. Empirically this category accounted for less than 2% of the total observed categories, and consequently did not contribute greatly to the overall analysis of the data. In the data analysis this category is included in with category 4 as it was of very low frequency.

(3) The categories of behaviour: Ferrets.

(a) Head in food receptacle (H). This category was similar to that in the rats, with a priority rule being applied to cover other behaviours that occurred simultaneously in this situation (i.e., in ferrets these other

behaviours included eating, licking and sniffing while the head was in the food receptacle). Unlike rats, the ferrets also adopted another behaviour towards the food receptacle, in which they lay prone and motionless with their heads resting in the receptacle. This second behaviour (Hi) was clearly different in that the animal lay prone, whereas in category H the animal was standing on all four feet and was engaged in active movement of the head and neck. This alternative behaviour (Hi) tended to occur over the latter portions of the inter-food interval, whereas H tended to occur about the period immediately following food delivery. Hi is further described in part (d) of this section. See Plate F 1.

(b) Eating: (E). Again, this behaviour followed a similar pattern to that observed in rats, with eating occurring in the food receptacle (and hence being scored as H) or immediately following H when the animals withdrew the food outside of the receptacle and consumed it in the chamber. The dog sausage used as food tended to crumble, so that the subjects often spent time licking up the small "crumbs" left over, and this behaviour was also scored as eating. See also Plate F 1.

As E invariably followed H early in the inter-food interval, and came under the overall category of *immediate food-oriented behaviour*, it was included in with H in the "collapsed" category of this name in the analysis (i.e. being shown as category 1).

(c) Sniffing: (S). This category describes a similar behaviour to that in rats, with rapid movement of the vibrissae and a directed head-orientation being the main

indices of this behaviour. Unlike this category in rats, there was a minimal relationship with ambulation, as sniffing behaviour tended to occur while the ferret was standing still (and remaining standing on all four feet). Thus the priority rule was rarely used in this instance. Sniffing has been accorded a single overall category in the analysis on the basis that, although it can be considered as an *active investigatory behaviour*, it differs from other such behaviours in ferrets in that it does not involve physical manipulation of objects in the environment (as is the case with scratching behaviour). In the analysis sniffing is shown as overall category 3. See Plates F2 and F3.

(d) Head in hopper but immobile: (Hi). This category described a common tendency for the ferrets to lie prone on the floor with their heads resting in the food receptacle when engaged in this behaviour, the subjects were motionless, and tended to remain in this posture until food was delivered. Hi is considered in relation to the next category. See Plate F 4.

(e) Immobile: (I). A similar category to Hi, except the animal's head is not resting in the food hopper. As with Hi, the ferrets often remained in this posture over long sequences of observation, only moving when food was delivered. As Hi and I were both similar in appearance and in temporal pattern (tending to occur most frequently towards the end of the inter-food interval) they were combined into the "collapsed" category of *stationary behaviours* (category 2 in the analysis). Unlike the "freezing" behaviour of rats, this behaviour in ferrets did not seem to be related to external noises etc., but rather

in response to the low temporal probability of food delivery. During bouts of this behaviour the animals rarely had their eyes closed. See Plates F 5 and F 6.

(f) Scratching: (Sct). A frequently observed behaviour in ferrets were bouts of protracted scratching at the floor of the chamber (where a piece of steel diamond mesh was fixed to provide a contact point for the drinkometer). Also very occasional scratches were directed at the food hopper, or the cover over the door to the activity wheel. The animals usually arched their backs, and scratched at the object with alternate sweeps of the fore-paws. During bouts of scratching the animal's head was directed towards the object being manipulated in this way. See Plate F 7.

(g) Scrabbling: (Scb). This behaviour was similar in frequency and temporal pattern to the previously described behaviour of scratching. It differed in topography in that the animals invariably lay on their sides, while directing this behaviour towards the door of the chamber. Scrabbling was always achieved by a sweeping motion of the fore-paws, the hind paws remaining outstretched and relatively immobile. The behaviour was most commonly observed when the ferrets heard external noises, or observed movement outside the chamber, and follows a similar pattern to "freezing" in rats in response to extraneous stimuli. (No plate available).

Because scratching (Sct) and scrabbling (Scb) were similar, in regard to temporal patterning, and to the use of fore-paws, these categories were "collapsed" into the overall category of *scratching behaviour* (category 4

Plate R1: Head in hopper and eating.

Plate R2: Ambulation.

Plate R3: Sniffing.

Plate R4: Rearing.

Plate R5: Drinking.

Plate R6: Grooming.

Plate R7: Grooming.

Plate R8: Stationary.

Plate F1: Head in food receptacle.

Plate F2: Sniffing.

Plate F3: Sniffing.

Plate F4: Head in hopper but immobile.

Plate F5: Immobile.

Plate F6: Immobile.

Plate F7: Scratching.

in the analysis).

(h) Miscellaneous: (M). As with the rats, this category was used to make the categories jointly exhaustive, and included a number of low frequency behaviours. These behaviours included defecation, licking at the drinking tube, rearing, grooming and ambulation. Unlike the behaviour of rats, the ferrets did not engage in grooming and rearing behaviours to any magnitude, and also tended to remain immobile for long periods, with a result that ambulation was not frequently recorded as a separate category. Ambulation, when it did occur, was mainly subsumed under the categories of sniffing and scratching, according to the priority rule. The miscellaneous category is shown in the analysis as category 5, since it occurred with a higher frequency than was observed with the rats.

(4) A summary of the overall categories: the organism-information approach.

In the foregoing description of the respective categories of behaviour, an overall summary has been applied to various groups of behaviour in order to simplify the analysis. This overall summary is presented in Table 6:1, and shows the abovementioned categories of behaviour in a simplified form. [2]

The overall summary has been based upon the organism-information approach (as discussed by Garcia, Clarke and Hankins, 1973) and also embodies elements of

2. To assist with the interpreting of the results, a detachable copy of Table 6:1 is located in a sleeve on the inside rear cover.

Table 6:1. A Summary of the categories of behaviour.

A: Rats.

Name of Behaviour	Symbol	Other Names	Overall - Category Classification.	Analysis Category No.
Head in food receptacle	H		*Immediate food - oriented behaviour.*	1.
Eating	E			
Ambulation	A	Locomotion	*Active investigatory behaviours.*	2.
Sniffing	S			
Rearing	R			
Drinking	D	Polydipsia/ Licking	*Schedule-induced polydipsia.*	3.
Grooming	G		*Stationary behaviours.*	4.
Stationary	F	Freezing		
Miscellaneous	M	Defecation, urination, pica, gnawing, climbing.	*Miscellaneous.*	4.
B. Ferrets.				
Head in food receptacle	H		*Immediate food-oriented behaviour.*	1.
Eating	E			
Head in food receptacle but immobile	Hi		*Stationary behaviours.*	2.
Immobile	I			
Sniffing	S		*Sniffing.*	3.
Scratching	Sct		*Scratching behaviour.*	4.
Scrabbling	Scb			
Miscellaneous	M	Defecation, licking, rearing, grooming, ambulation.	*Miscellaneous.*	5.

Staddon and Simmelhag's (1971) concepts relating to adaptive behaviour and principles of behavioural variation. Garcia *et al* comment that an organism can be seen,

> "as an information-seeking entity operating in a complex environmental field"

Accordingly the behaviour of the organism can be considered as,

> "as a *patterned sequence* beginning with *arousal and orientation*, passing through a *coping appetitive phase*, and terminating in a *consummatory phase*. If coping behaviour is blocked before consummation, or if consummation is delayed, then the segments of the original sequence may be *displaced*, with adjunctive behaviours directed at features of the environment which have *demand or incentive* characteristics. For example, the hungry rat waiting for his intermittent food reward drinks water because it is there. The hungry pigeon walks in circles because it must wait within the confines of the Skinner box". (author's italics).

This formulation sees the various behaviours that occur between successive food deliveries as a form of information-seeking, in that the animal develops meaningful relationships between these behaviours and the likelihood of food delivery.

This proposal by Garcia *et al* embodies similar principles to Staddon and Simmelhag's account of "superstitious" behaviour. In this latter account, adjunctive behaviours are seen as occurring when the appropriate stimuli (i.e. goal objects) are present in the period following food delivery (where there is a low probability of reinforcement, or food delivery). This period is associated with the occurence of interim activities, and these activities are seen to resemble appetitive behaviour.

Adjunctive behaviours and displacement behaviours are considered to be very similar to interim activities in Staddon and Simmelhags' theory, as exemplified by the following statement:

> "Finally, our account of the adaptive significance of adjunctive behaviour, as a reflection of the intergrative capacities of the organism which enable it to strike an efficient balance among a number of activities, finds a counter-part in McFarlands' (1966) account of the significance of displacement behaviour:
>
> ' *Thus it is suggested that the functional significance of displacement activities is that they are the by-product of a mechanism which enables animals to break away from a specific course of action, when progress in that course of action comes to a standstill (p. 231)*'

> We conclude, therefore, that interim, adjunctive and displacement behaviours may be grouped together on the basis of similar functional properties, similar probable causal factors, and similar adaptive role".

This statement has significance beyond the theoretical relationship between interim, adjunctive and displacement behaviours, as it provides a working hypothesis about the likely behaviour of various species during the period following food delivery in the experimental situation. Since these three phenomena appear in "thwarting" or "conflict" situations, in a time when the chances of feeding are slight, and "enable the animal to break away from a specific course of action", then the behaviour of different species may reflect the temporal and sequential patterning commonly found with these phenomena. This patterning should occur in the period following food delivery (i.e. the period of interim activities), and may reflect the patterns appropriate to the ecological characteristics of these differing species.

(D) A Comparative Observational Experiment.

The behaviour of food deprived rats and ferrets individually placed on a FF1 100-sec schedule of food delivery was observed and recorded according to the categories described in the previous section.

Subjects:

(I) Rats: Two experimentally naive male hooded rats aged 180 days served. These subjects respectively weighed 294 gms (R1) and 337 gms (R2).

(II) Ferrets: Two experimentally naive male ferrets aged 330 days served. Their respective weights were 1073 gms (F1) and 1146 gms (F2).

Apparatus:

The rats were tested in *Rat Chamber 2*, under similar conditions as in the previous studies described in Chapter 4 (experiments 2 and 3), with the exception that the licking-tube was absent. The ferrets were tested in the *Ferret Chamber* under similar conditons as described in Chapter 5, with the drinking tube continuously available. The ferret activity wheel was not available during this experiment.

Procedure:

Both the rats and ferrets were weighed, and food deprived to 80% and 85% F.F.W. respectively over a period of 7 days. The rats then received a 30 minute habituation session in the apparatus, with 50 food pellets being placed in the food receptacle, in order that the subjects familiarise themselves with the location and taste of the food. The rats then received 17 daily sessions, on a FF1 100-sec schedule, with 100 pellets being delivered per session. The subjects were observed on days 1, 3, 8, 12 and 15. On day 17 the subjects were photographed.

The ferrets were placed in the apparatus for a 30

minute habituation session on day 1 of the rat experiment in order that the observational sessions be staggered over different days. During the habituation session 50 pieces of food were placed in the receptacle to familiarise the subjects to the location and the type of food. The ferrets then received 16 daily sessions on a FF1 100-sec schedule, with 100 pieces of food being delivered on each session. The ferrets were observed on days 1, 3, 8 and 12, and were photographed on day 16.

The observational sessions comprised three separate sampling periods during each daily session, in which the behaviour of each subject was recorded every 2 seconds for a duration of 10 food cycles (i.e. 1,000 seconds, 500 observations) so that a total of 1,500 observations per session were obtained over a total of 30 cycles of food delivery. The sampling periods were spaced evenly over each daily session, and were comprised of food cycles 5-14, 45-54, and 85-94. These spacings of the sampling periods were designed as controls for within session effects.

The selection of observation days was based upon the previous studies on schedule-induced polydipsia in rats, where this behaviour appeared to reach asymptote around days 6-8 under similar experimental conditions. Thus days 1 and 3 ought to reflect the early development of schedule-induced polydipsia, and days 8 and 12 should show this behaviour at full strength. The observations on day 15 with the rats were of a special condition introduced to examine the effects of removing the drinking tube (and thereby denying the animals the opportunity to show polydipsia). The drinking tube was removed on day 13 in this

condition, in order that other behaviours might develop over the ensuing 2 days.

The choice of observation days for the ferrets was determined by the necessity to maintain an equivalent situation as that with the rats. The ferrets did not have any special conditions imposed on day 15.

Apart from recording 1,500 observations per subject in each daily session, additional data were obtained from the rats on the number of licks, and amount of water consumed, as polydipsia developed. This information served as comparison data with the previous experiments on schedule-induced polydipsia.

Method of analysis. The data were analysed by two different techniques.

(a) The occurence of each specific category as a percentage contribution to the total data pool. This measure was a gross assessment of which categories changed in frequency over successive sessions.

(b) The temporal distributions of each overall category of behaviour (e.g. *immediate food-oriented behaviour*, schedule-induced polydipsia, etc.) over each session. Instead of presenting the distributions for each overall category separately, a modified form of presentation was adopted whereby the *cumulative* frequency of successive overall categories is shown for each temporal 'bin' in the cycle. Thus the observed frequency of any given overall category can be assessed in relation to *all* the other overall categories simultaneously. It was felt that this presentation would simplify the interpretation of the data,

as well as giving a total picture of which categories contributed most (or least) at any point in the food cycle, thereby indicating the presence of any clear patterning of the various groups of behaviours observed.

(1) The Rat Experiment.

Results:

(a) Percentage occurrence of each category. These results are presented in Table 6:2, and show the percentage occurrence of each category for both subjects over all sessions (including day 15 when the drinking tube was absent), and this information is further presented in Figure 6:1.

(b) Schedule-induced polydipsia. The number of licks and water intake per daily session is presented in Table 6:3. These data indicate that the subjects developed polydipsia to a similar pattern and magnitude as the previous subjects (see Chapter 4).

(c) The cumulative temporal distribution of over-all categories. These data are presented in Figures 6:2 a-e (subject R1) and 6:3 a-e (subject R2). In these figures various overall categories are coloured so as to assist in their discriminability; these colours do not imply any special significance of the respective categories beyond making them clearer.

Discussion:

(a) Percentage occurrence of each category. The results indicate that some categories of behaviour appear relatively stable in occurrence over sessions (H, E, and

Table 6:2. Percentage occurrence of categories per session.

Subject R1.

Category	Day 1	Day 3	Day 8	Day 12	Day 15
H	8.66	11.46	9.73	9.14	13.20
E	4.26	2.06	4.53	3.20	7.53
A	7.74	15.06	11.26	9.09	4.40
S	26.60	17.80	18.86	18.14	21.27
R	3.34	15.35	5.80	4.00	2.07
D	8.20	22.40	28.26	35.66	-
G	29.66	9.54	13.46	13.14	23.60
F	11.27	5.06	7.73	6.80	27.73
M	0.27	1.27	0.03	0.86	0.20
Subject R2.					
H	6.40	10.73	6.73	8.93	8.27
E	5.40	2.94	6.26	3.20	8.07
A	10.33	17.93	5.40	7.93	2.46
S	22.80	17.13	24.46	15.26	18.54
R	6.07	14.53	2.53	3.86	1.13
D	10.94	18.33	25.93	33.94	-
G	18.33	8.94	15.13	18.60	41.80
F	19.46	8.20	11.66	6.54	19.40
M	0.27	1.27	1.86	1.74	0.33

Figure 6:1 Percentage occurence of respective categories.

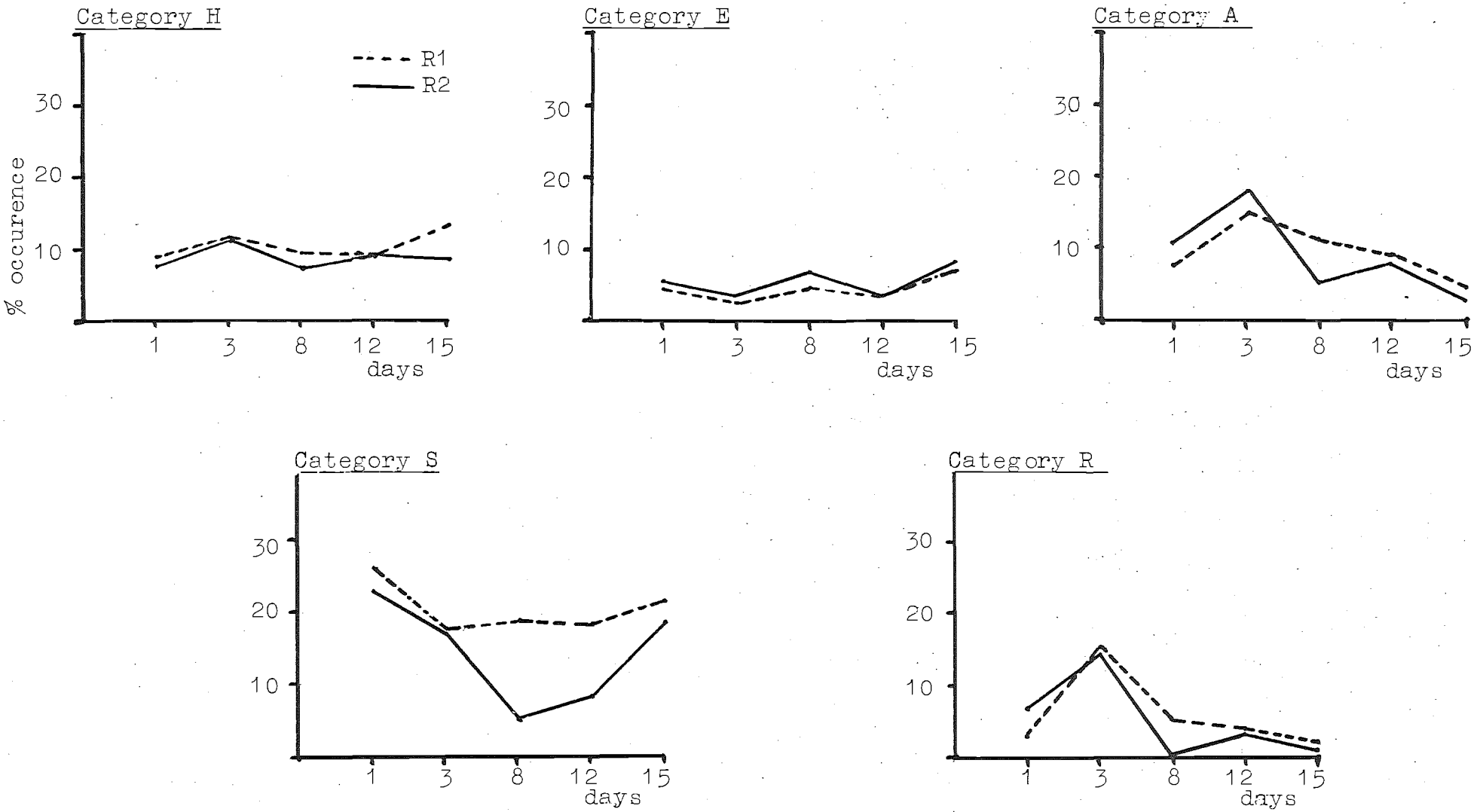
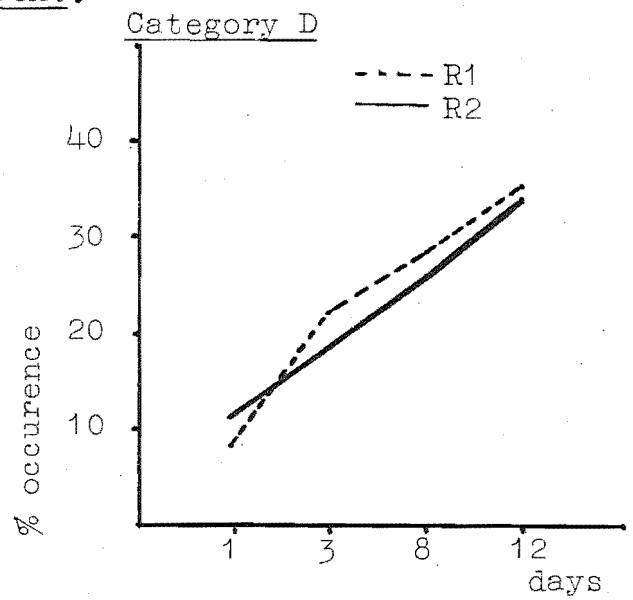
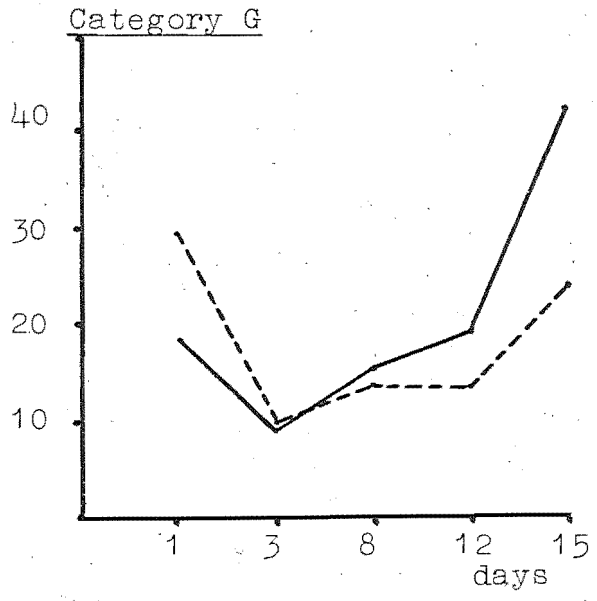
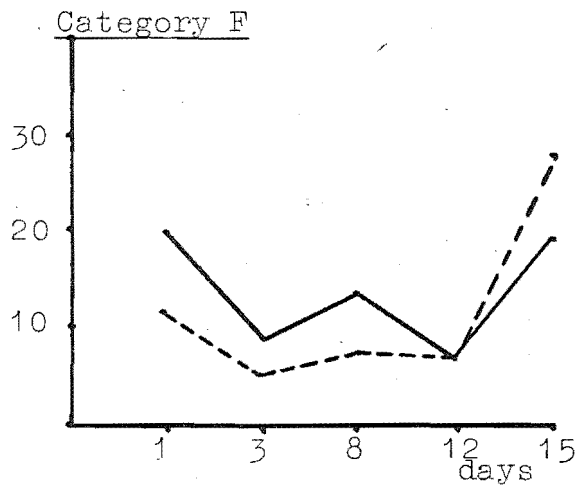


Fig. 6:1 Cont.


Category D
R1
R2
40
30
20
10
% occurence
1
3
8
12
days


Category G
40
30
20
10
1
3
8
12
15
days


Category F
30
20
10
1
3
8
12
15
days

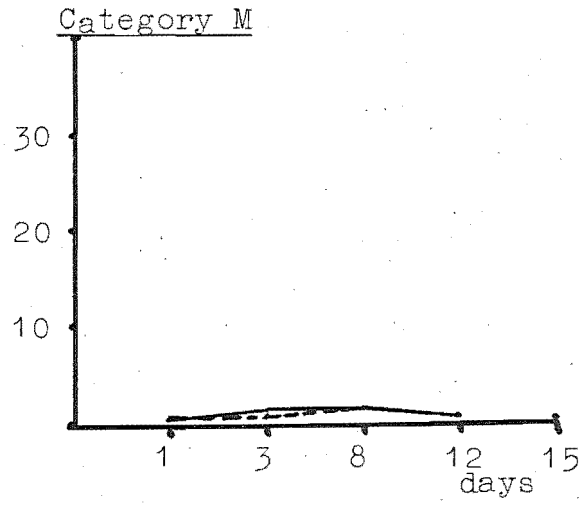
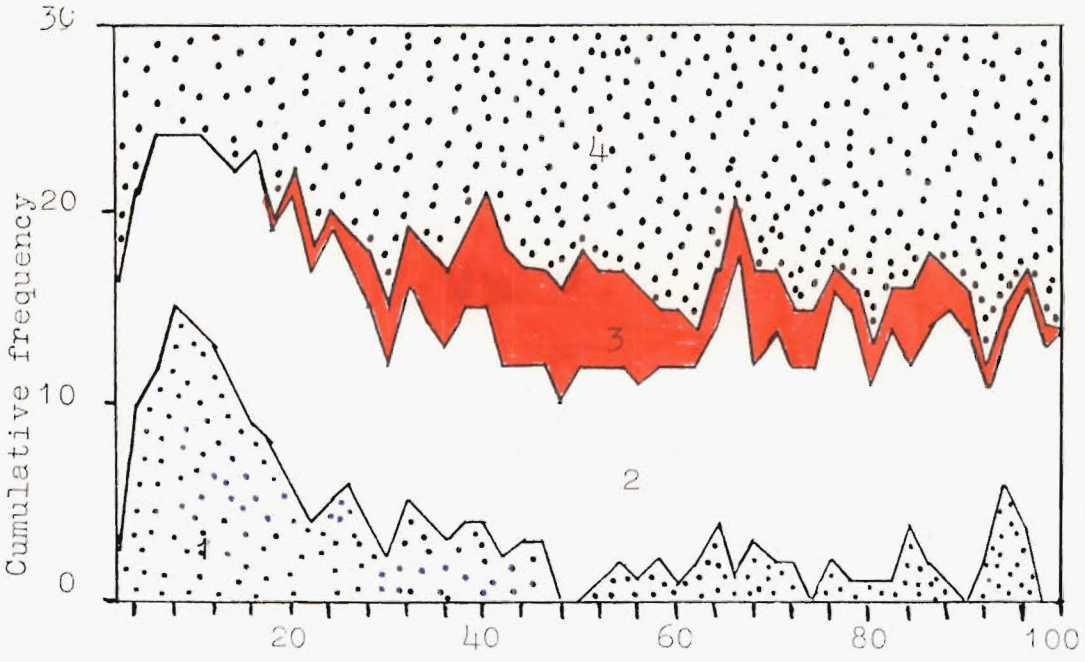

Category M
30
20
10
1
3
8
12
15
days

Table 6:3. Water intake and number of licks per subject each session.

	R1		R2	
Session	Number of licks.	ml's consumed.	Number of licks.	ml's consumed.
1	1946	9.3	1398	6.6
2	2791	12.4	2313	9.1
3	4093	17.9	2877	14.7
4	5271	21.2	4865	23.8
5	7044	24.8	7402	27.5
6	7380	25.3	9418	29.0
7	8185	28.1	10068	33.8
8	9607	34.3	9716	34.7
9	9482	33.8	12485	35.2
10	9871	36.7	10611	33.4
11	10563	39.4	1170	34.1
12	9945	36.5	12562	37.2

SAMPLE FIGURE: Cumulative temporal distribution of overall categories (RATS).

Cumulative frequency over 30 cycles of food delivery of respective overall categories versus inter-food interval.



1: Immediate food-oriented behaviours.

2: Active investigatory behaviours.

3: Schedule-induced polydipsia.

4: Stationary behaviours and Miscellaneous.

Subject R1. Figure 6:2
Subject R2. Figure 6:3

a: day 1
b: day 3
c: day 8
d: day 12
e: day 15

Figure 6:2 (a) Subject R1.

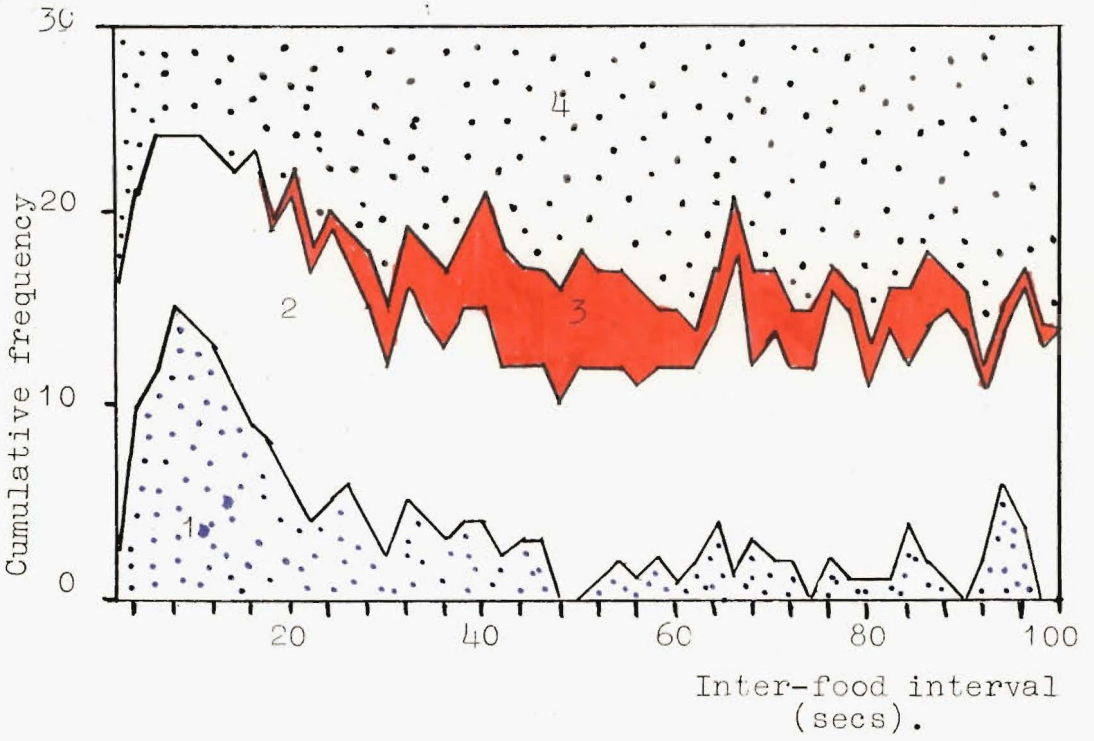


Figure 6:3 (a) Subject R2.

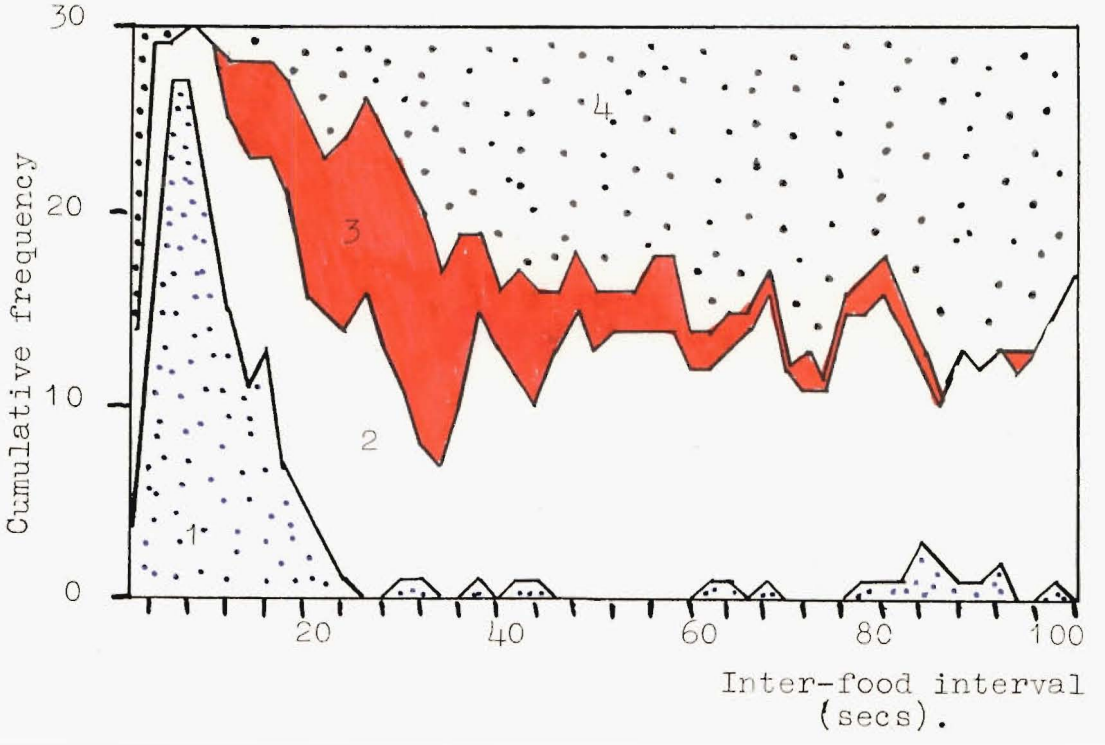


Figure 6:2 (b) Subject R1.

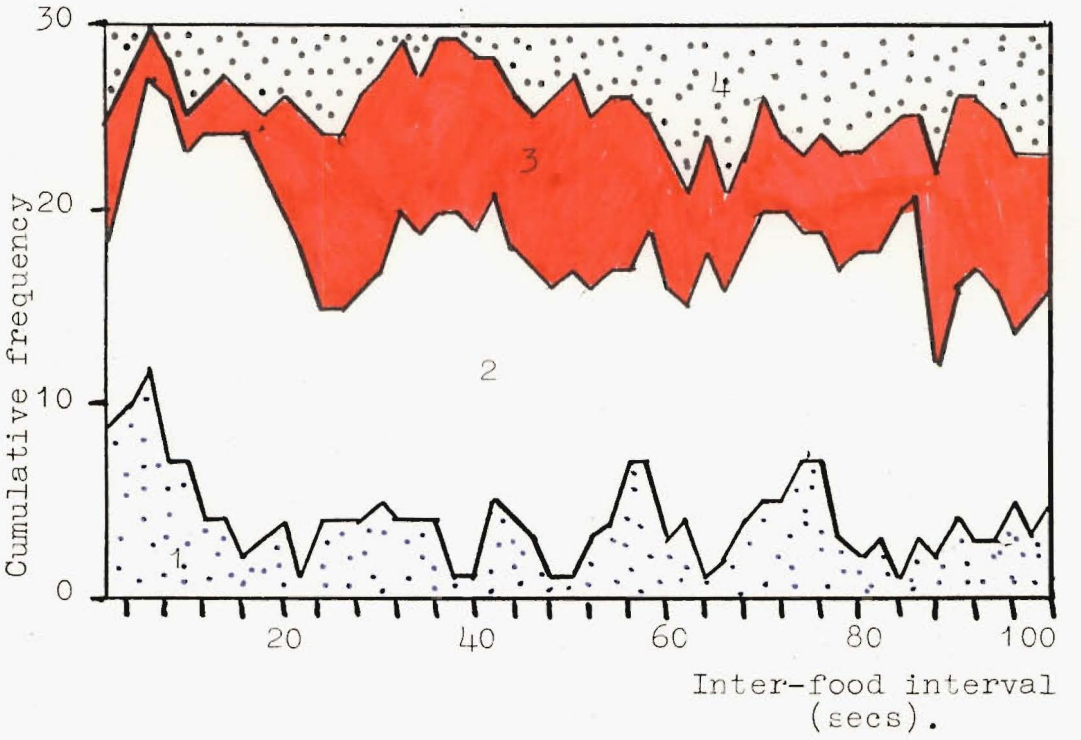


Figure 6:3 (b) Subject R2.

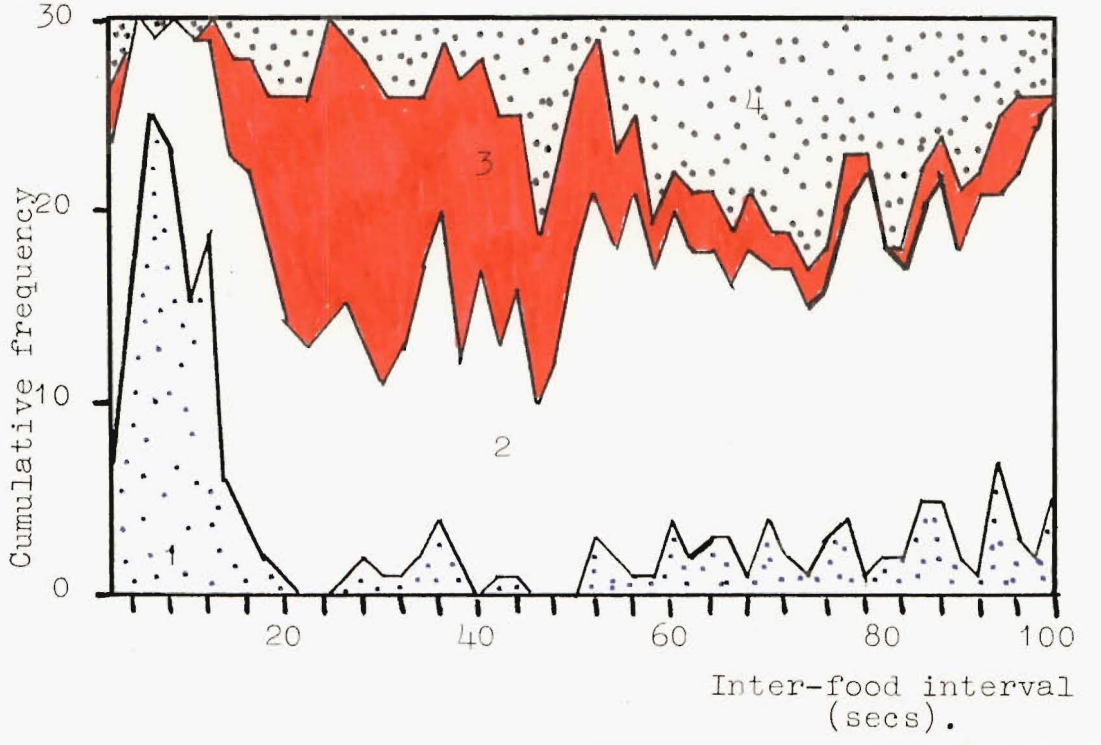


Figure 6:2 (c) Subject R1.

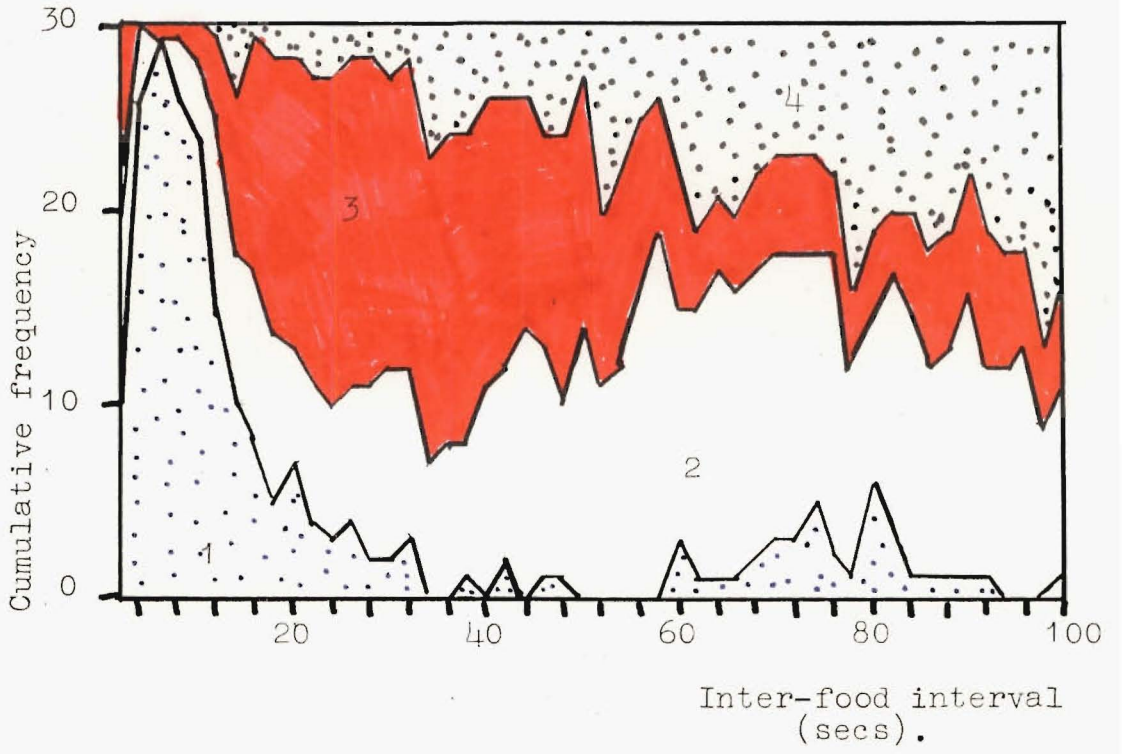


Figure 6:3 (c) Subject R2.

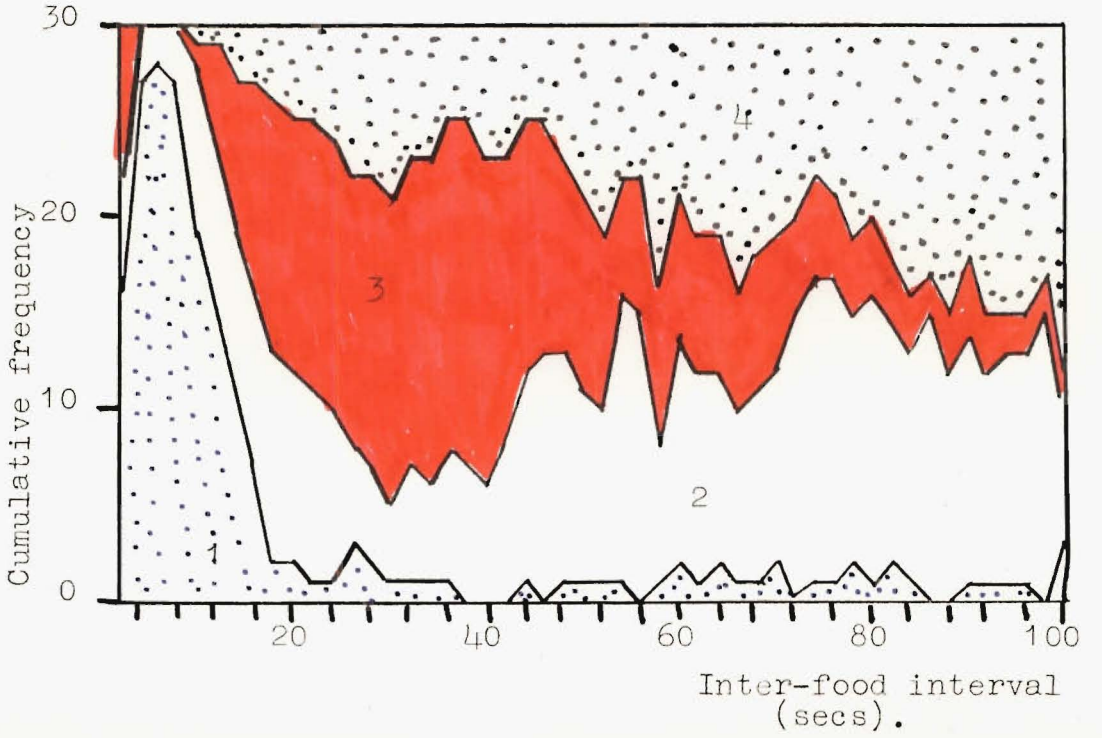


Figure 6:2 (d) Subject R1.

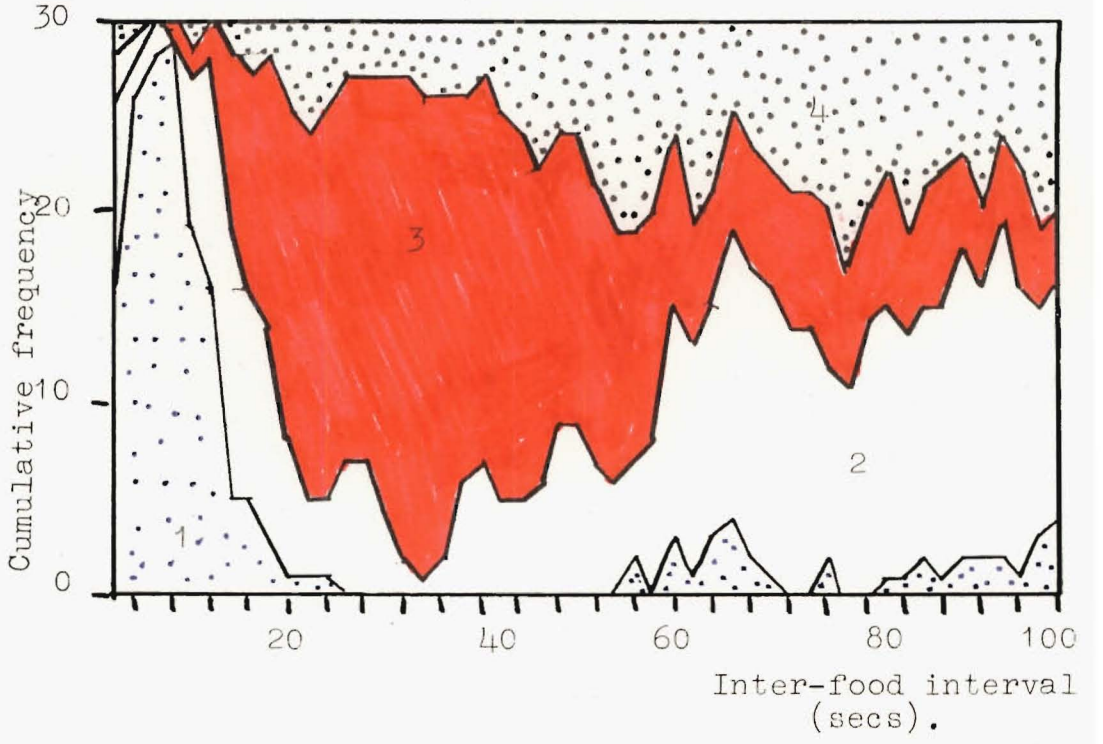


Figure 6:3 (d) Subject R2.

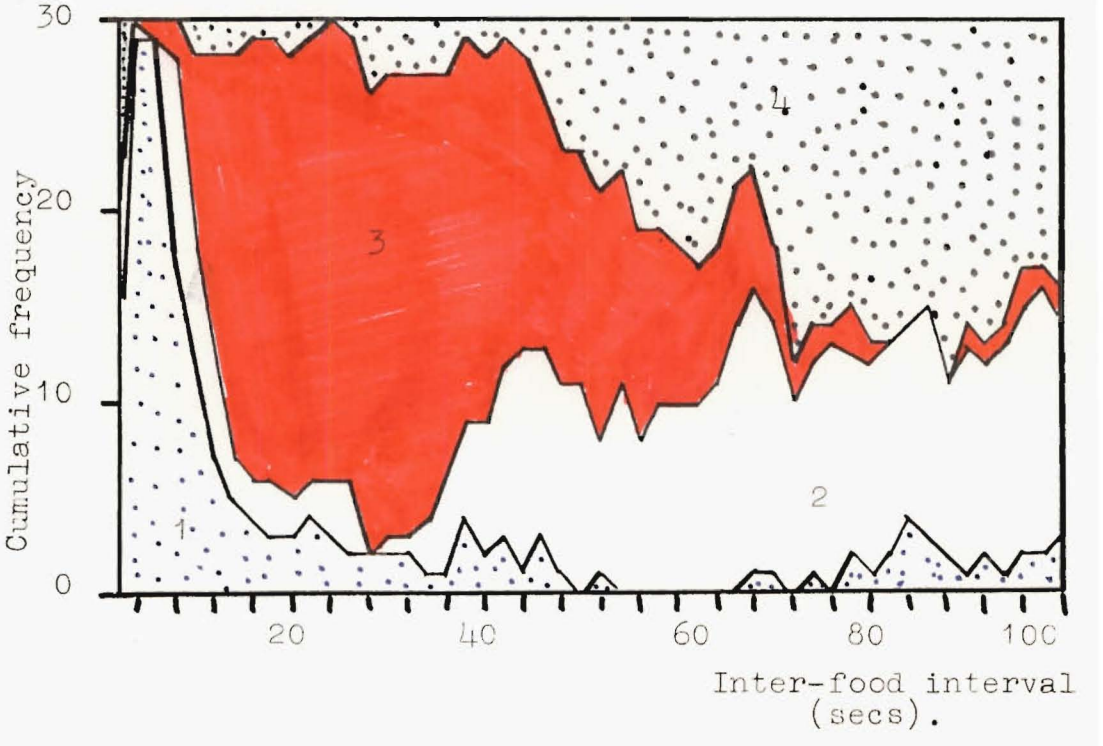


Figure 6:2 (e) Subject R1.

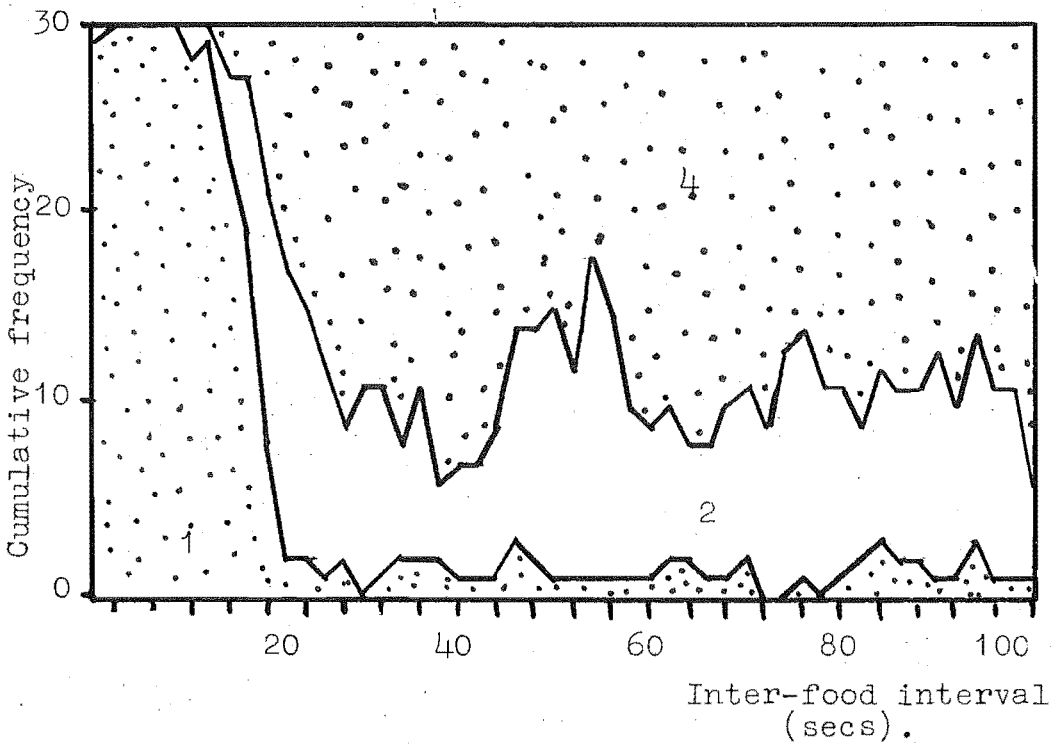
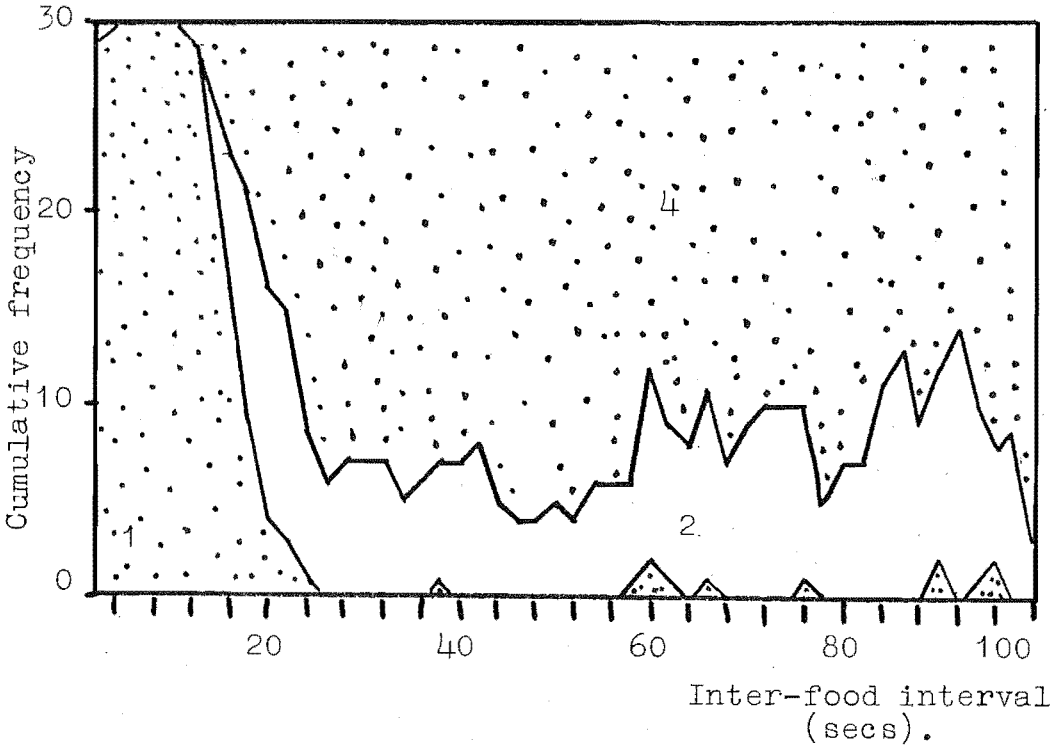


Figure 6:2 (e) Subject R2.



M) as would be expected, since H and E are tied in closely with the delivery of food and the rate of its consumption, while M was of a very low frequency and no trends can be discerned from it.

The categories A and R (*active investigatory behaviours*) indicate an initial low level on day 1, followed by an increase on day 3, and then a general decline, as may be expected as the subjects gained experience with the experimental environment (i.e. this might be considered as an instance where the "information content" of the environment becomes diminished with exploration and familiarity). The other *active investigatory behaviour*, S, shows a high incidence on day 1, then appears to decline more slowly (allowing for the individual differences in this category).

As would be expected of an adjunctive behaviour, the percentage occurrence of drinking increases with the development of schedule-induced polydipsia. This trend is also reflected in the data from Table 6:3 showing the experimental sessions water intake and number of licks.

Categories G and F reveal an overall similarity (reflecting their overall category of *stationary behaviours*) in that they initially occur with a high frequency (suggesting a reaction to the "novelty" of their environment), then decline. Significantly, these two behaviours were the most effected by the removal of the drinking tube, and show a great increase in occurrence on day 15. This implies that they are closely related to displacement activities, since they occur with the highest frequency,

(i) when the environment is "new" (and has not been fully investigated), and

(ii) When the familiar environment of the experimental chamber undergoes a reduction in "stimulus complexity" [3] with the drinking tube being removed (i.e. the animal has even less potential activities to engage in).

However, since the data are ipsitive, then care in interpreting trends is necessary in the case of the data from day 15; since changes in the percentage occurrence of all behaviours must be expected when one behaviour (schedule-induced polydipsia, which accounted for over 30% of all categories on the previous session) is removed from the sample. Despite this caution, it is significant that G and F most reflect the changed conditions on day 15, as opposed to the other remaining categories.

(b) The cumulative temporal distributions of the overall categories. Figures 6:2 a-e and 6:3 a-e reveal an interesting pattern over the successive days of observation.

Category 1 - (*immediate food-oriented behaviours*) shows the learning of the temporal probability of food delivery, since the early sessions indicate a pattern of sporadic occurrence of this behaviour throughout the food cycle. However, the latter sessions show a very high probability of this behaviour occurring after food delivery, usually to the exclusion of other behaviours, followed by a rapid decline to a minimal level throughout the rest of the inter-food interval.

3. "Stimulus complexity" in this sense refers to the number of stimulus items in the experimental environment with which the animal may interact.

Category 2 - (*active investigatory behaviours*) appears to occur with equi-probability throughout the period following food delivery in the early sessions, but changes in pattern as schedule-induced polydipsia develops, when it is more frequently observed at the end of the inter-food interval. Thus, this category is displaced to a greater extent by the development of polydipsia. As noted in the previous discussion, the removal of the drinking tube did not markedly effect the distribution and magnitude of this category.

Category 3 (schedule-induced polydipsia) follows the expected pattern of a behaviour that develops to asymptote, and occurs in the period following food delivery. The "post-pellet" locus of this phenomenon is clearly demonstrated on days 8 and 12, where a substantial portion of time immediately following food consumption is occupied by this behaviour. Of added interest is the diminished occurrence of polydipsic behaviour towards the latter portions of the inter-food interval, indicating that this behaviour is not an exclusive post-pellet phenomenon.

Category 4 (*stationary behaviours*) initially occurred at a high frequency in the period following food delivery on day 1, with a decline on day 3 (when category 2 shows an increase, as noted in the previous discussion). With the development of polydipsia, category 4 shows a similar pattern to category 2, in that both these categories appear to be displaced by the drinking, and tend to occur with increasing probability towards the end of the inter-food interval. On days 8 and 12 both categories 2 and 4 show a near equal probability of occurrence.

With the drinking tube removed on day 15, category 4 expanded to occupy the space left by the absence of drinking behaviour, and as previously discussed, this appears to be in response to a decline in the complexity of the environment under this condition.

In general, these data indicate that as the subject learns the temporal probability of food delivery, schedule-induced polydipsia develops to occupy the period following eating and tapers off towards the latter portion of the interval, when active investigatory behaviours and stationary behaviours increase in frequency. The removal of the drinking tube appears to promote an increase in stationary behaviours, possibly because of the lack of a suitable object (i.e. the drinking tube) to direct behaviour towards.

(2) The Ferret Experiment.

Results:

(a) Percentage occurrence of each category. These results are presented in Table 6:4, and are further shown in Figure 6:4.

(b) The cumulative temporal distribution of overall categories. These data are presented in Figures 6:5 and (subject F1) and 6:6 a-d (subject F2). As with the rat data, various overall categories are coloured in to assist in their discriminability.

Discussion:

(a) Percentage occurrence of each category. As with the results from the rats, H and E show a stable level of occurrence as would be expected given the limited

Table 6:4. Percentage occurence of each category per session.

Subject F1

Category	Day 1	Day 3	Day 8	Day 12
H	12.40	12.33	11.40	9.20
E	6.47	5.07	4.74	5.47
Hi	30.66	29.73	25.93	36.80
I	8.07	14.80	17.86	17.27
S	14.40	13.93	12.93	8.80
Sct	9.47	9.94	13.53	10.13
Scb	13.06	4.26	4.07	6.26
M	5.47	9.94	9.54	6.06
Subject F2				
H	18.20	10.86	10.81	9.87
E	2.67	4.47	7.07	5.87
Hi	36.26	25.06	31.60	38.53
I	4.27	6.74	11.67	13.06
S	17.87	11.00	17.30	9.47
Sct	6.33	10.47	8.94	8.40
Scb	1.73	21.80	6.74	9.60
M	12.67	9.60	5.87	5.20

Figure 6:4 Percentage occurence of respective categories.

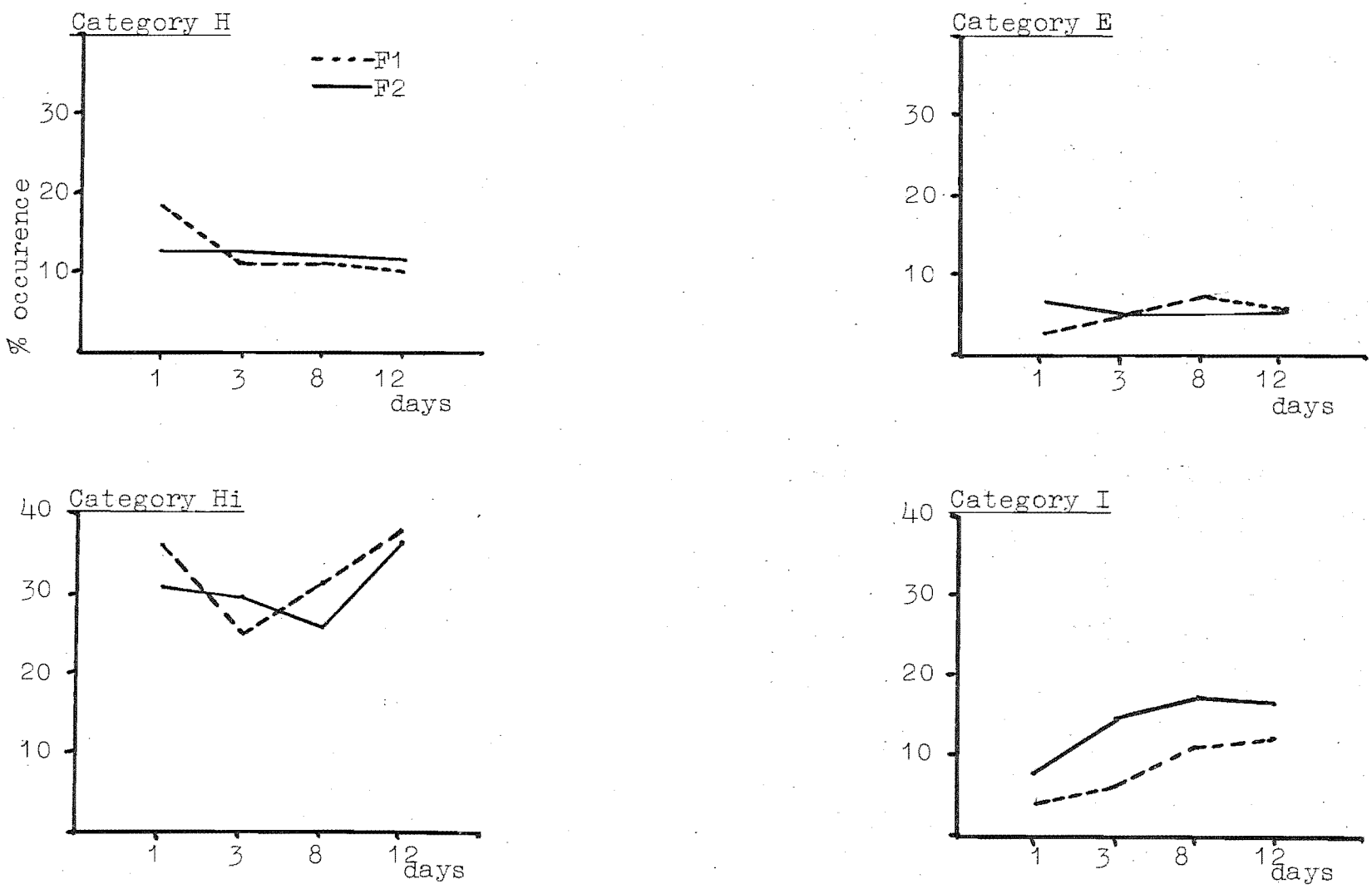
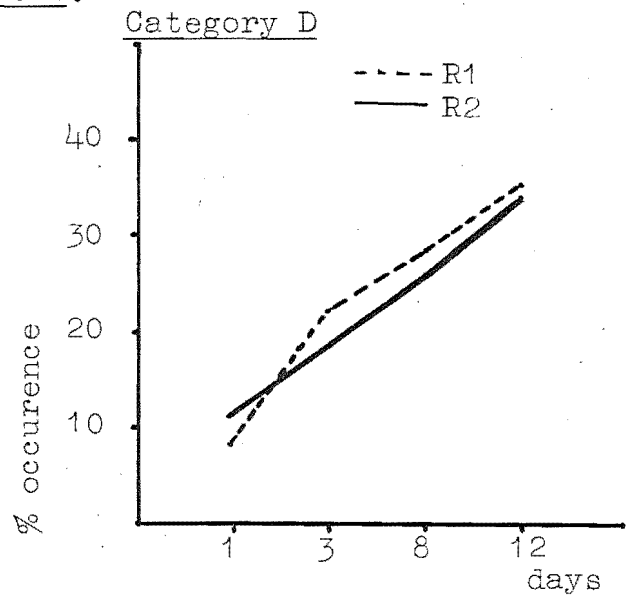
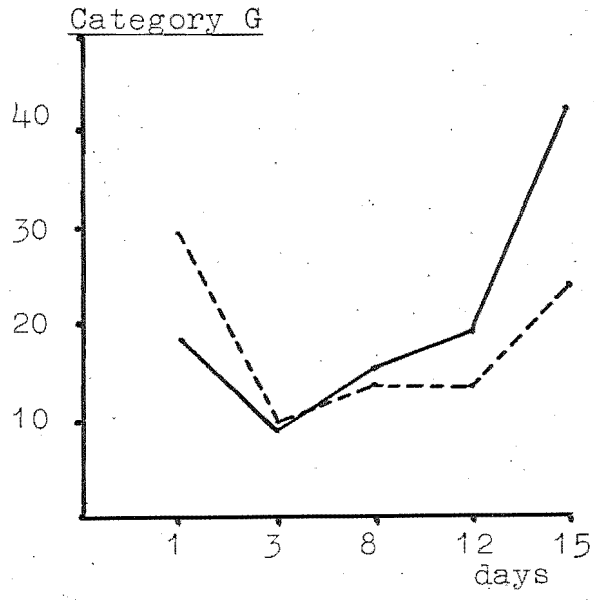
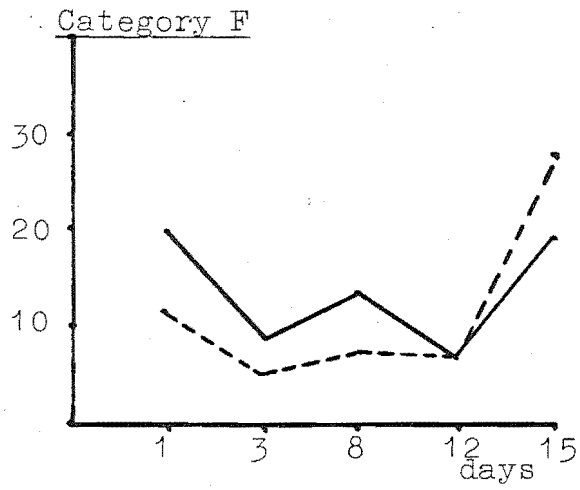
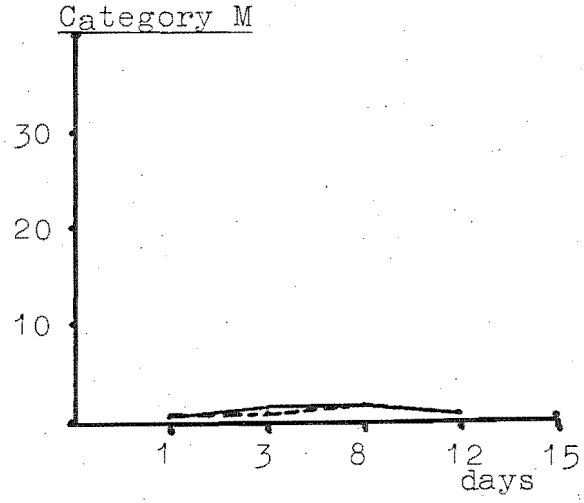


Fig. 6:1 Cont.


Category D
R1
R2
40
30
20
10
% occurence
1
3
8
12
days

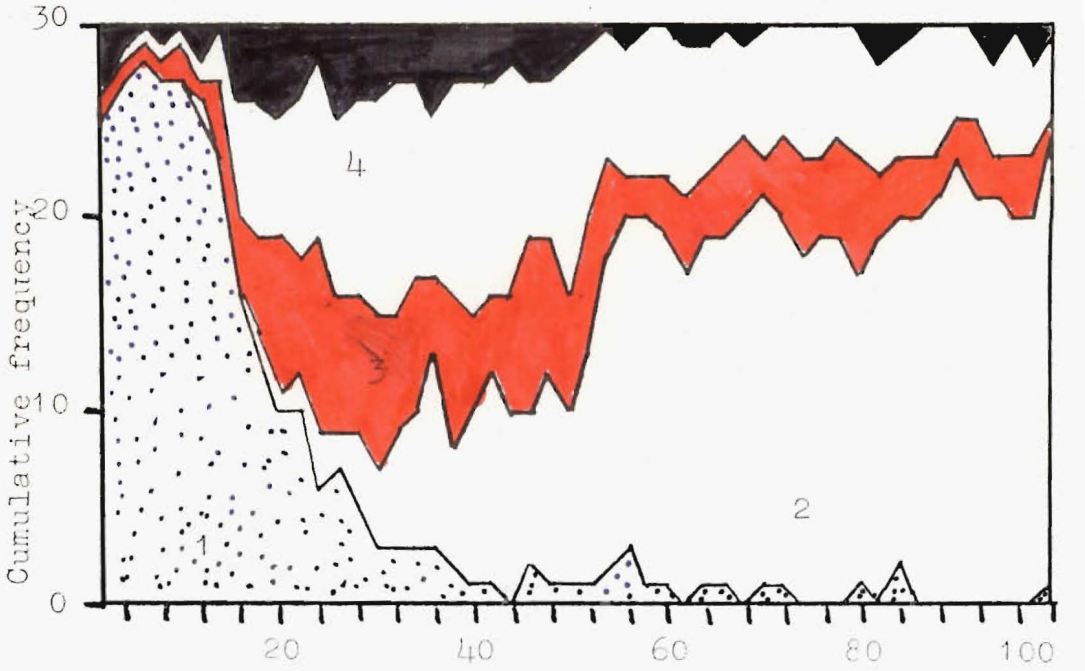

Category G
40
30
20
10
1
3
8
12
15
days


Category F
30
20
10
1
3
8
12
15
days


Category M
30
20
10
1
3
8
12
15
days

SAMPLE FIGURE: Cumulative temporal distribution of overall categories (FERRETS).

Cumulative frequency over 30 cycles of food delivery of respective overall categories versus inter-food interval.



1: Immediate food-oriented behaviours.

2: Stationary behaviours.

3: Sniffing.

4: Scratching behaviour.

5: Miscellaneous.

Subject F1. Figure 6:5

Subject F2. Figure 6:6

a: day 1

b: day 3

c: day 8

d: day 12

Figure 6:5 (a) Subject F1.

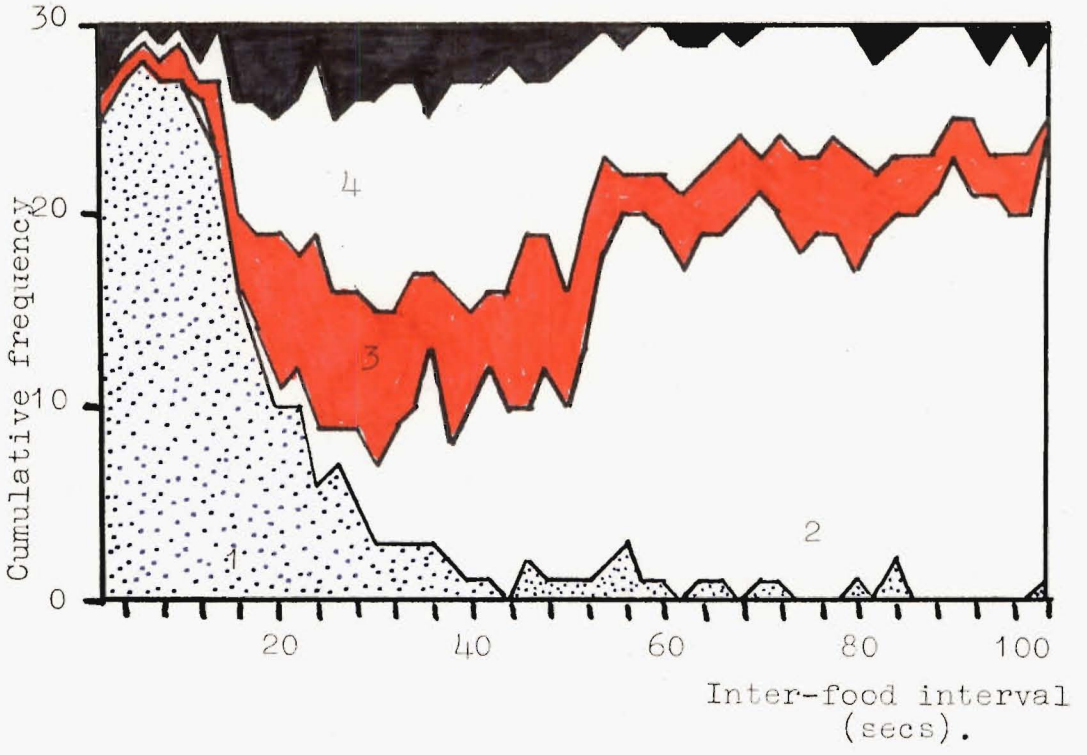


Figure 6:6 (a) Subject F2.

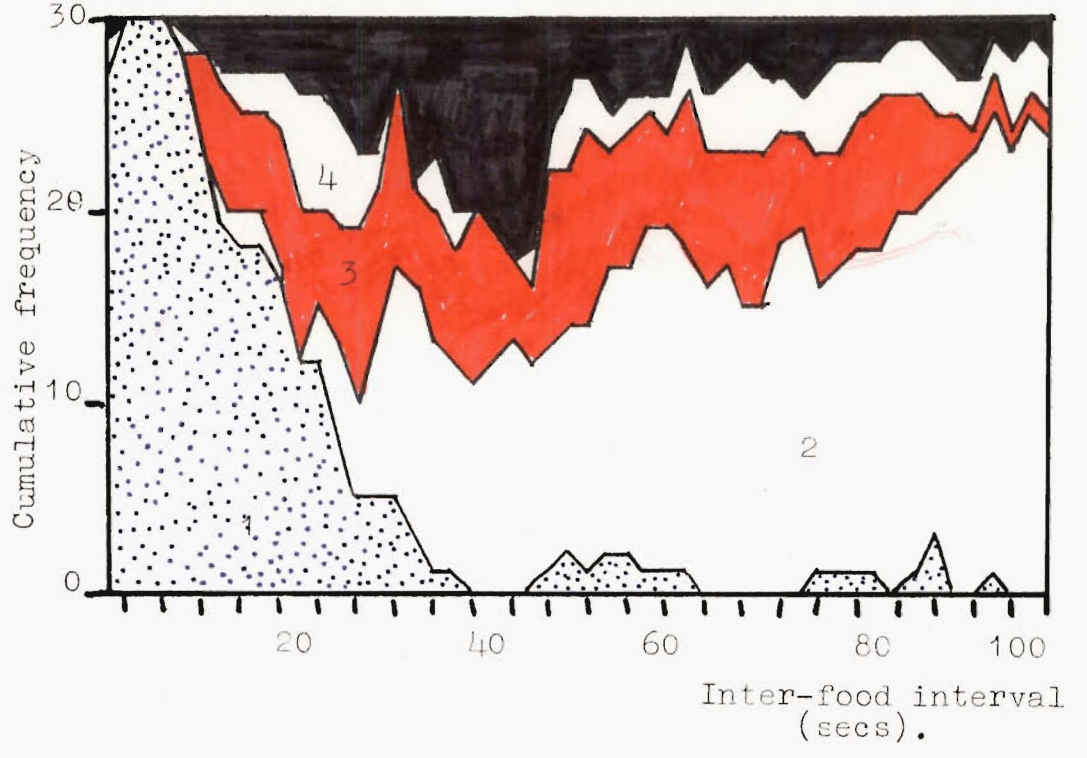


Figure 6:5 (b) Subject F1.

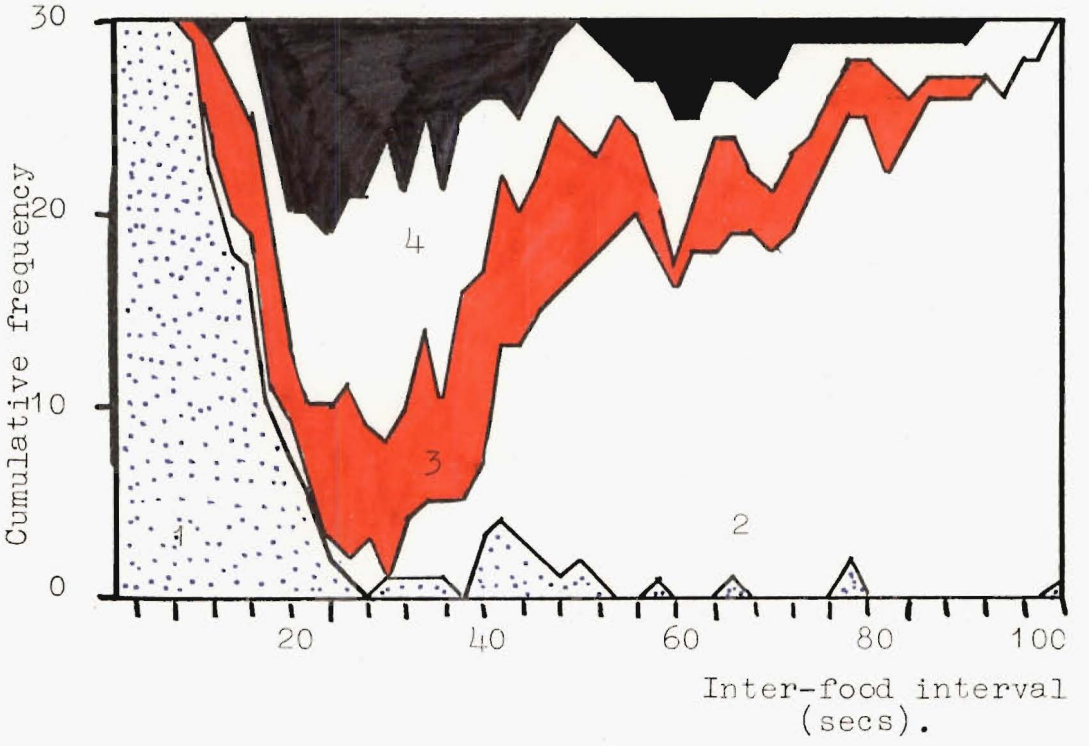


Figure 6:6 (b) Subject F2.

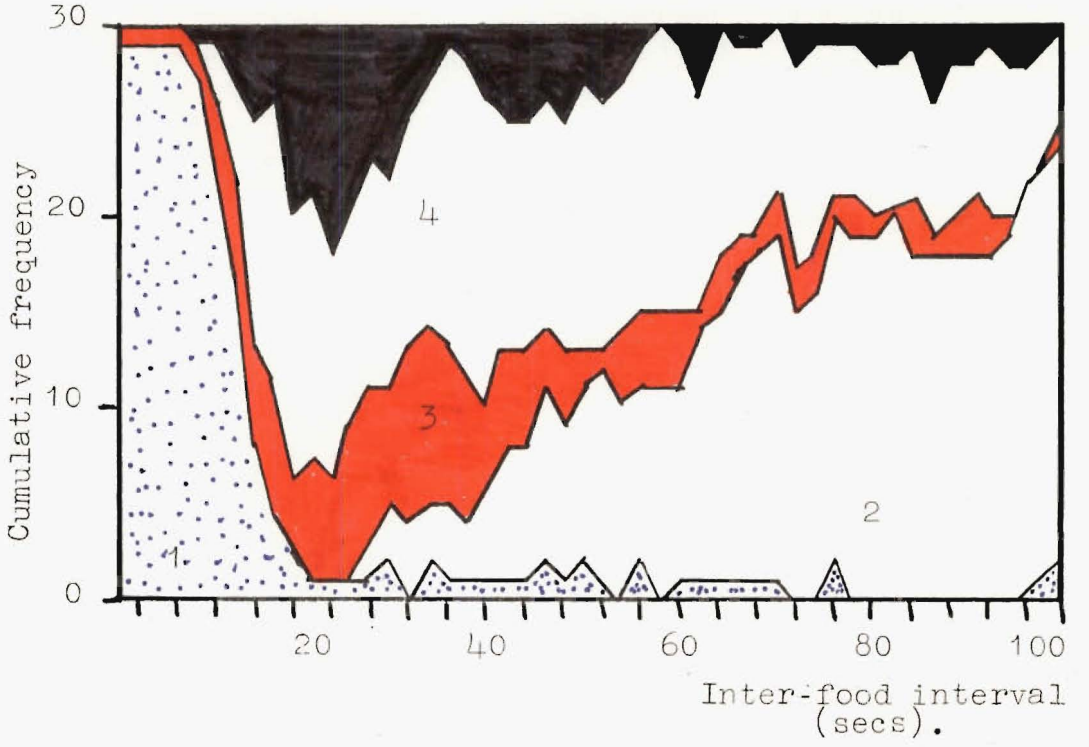


Figure 6:5 (c) Subject F1.

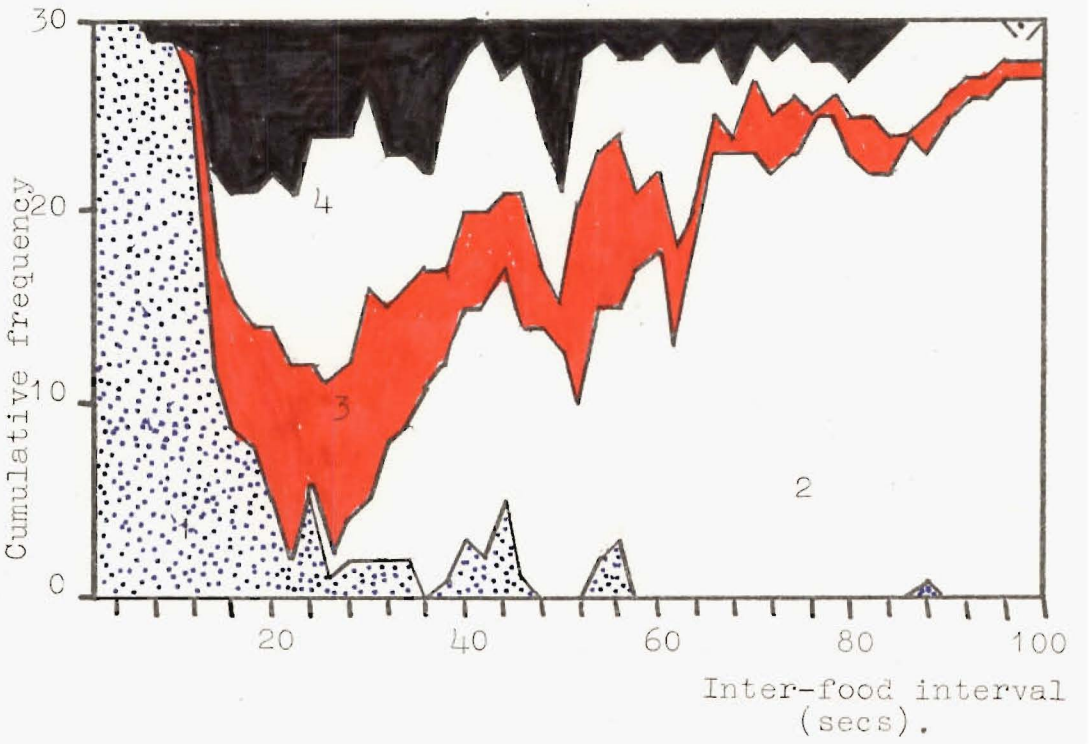


Figure 6:6 (c) Subject F2.

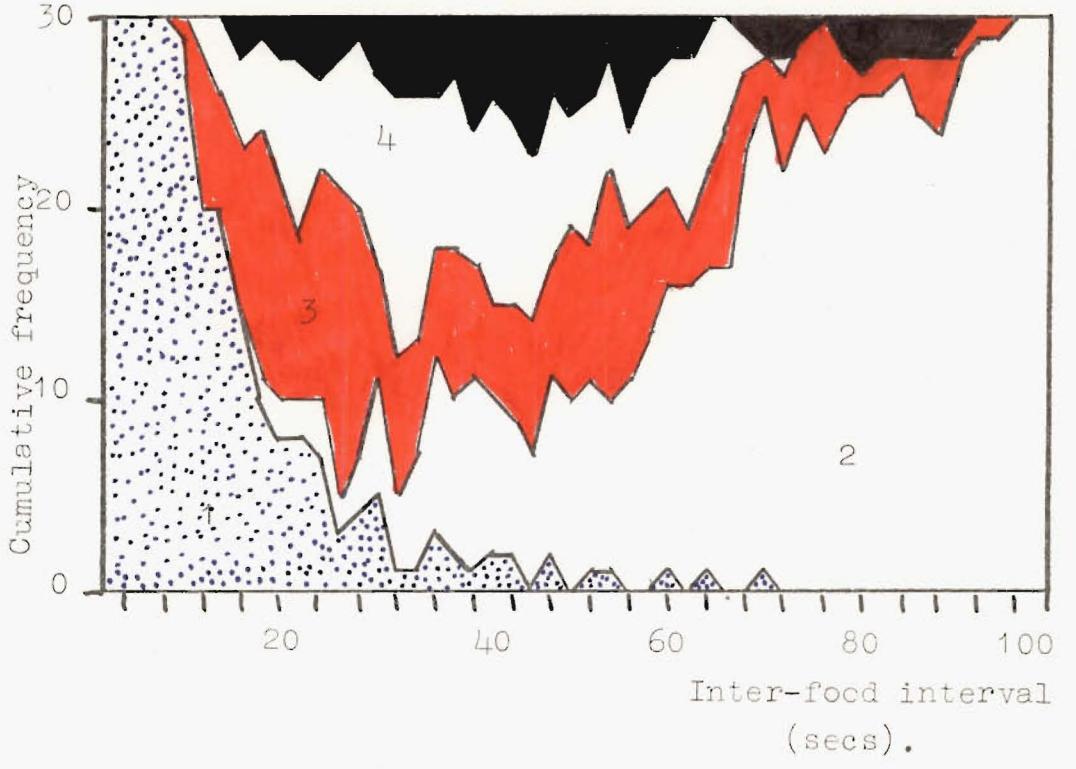


Figure 6:5 (d) SubjectF1.

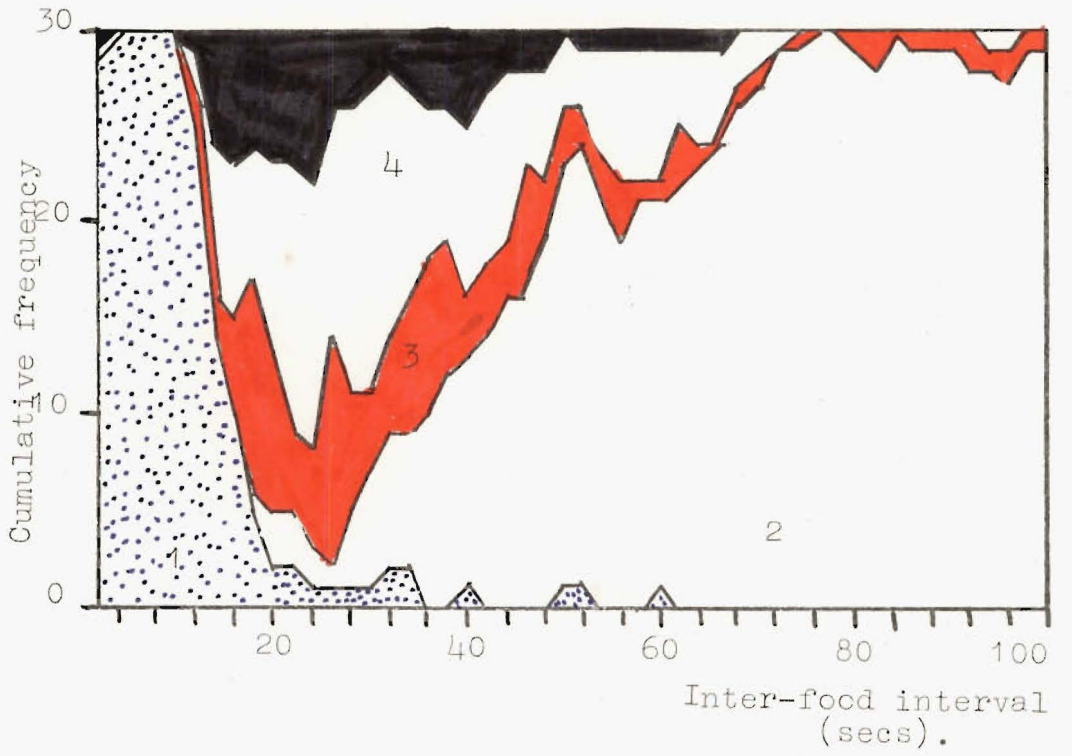
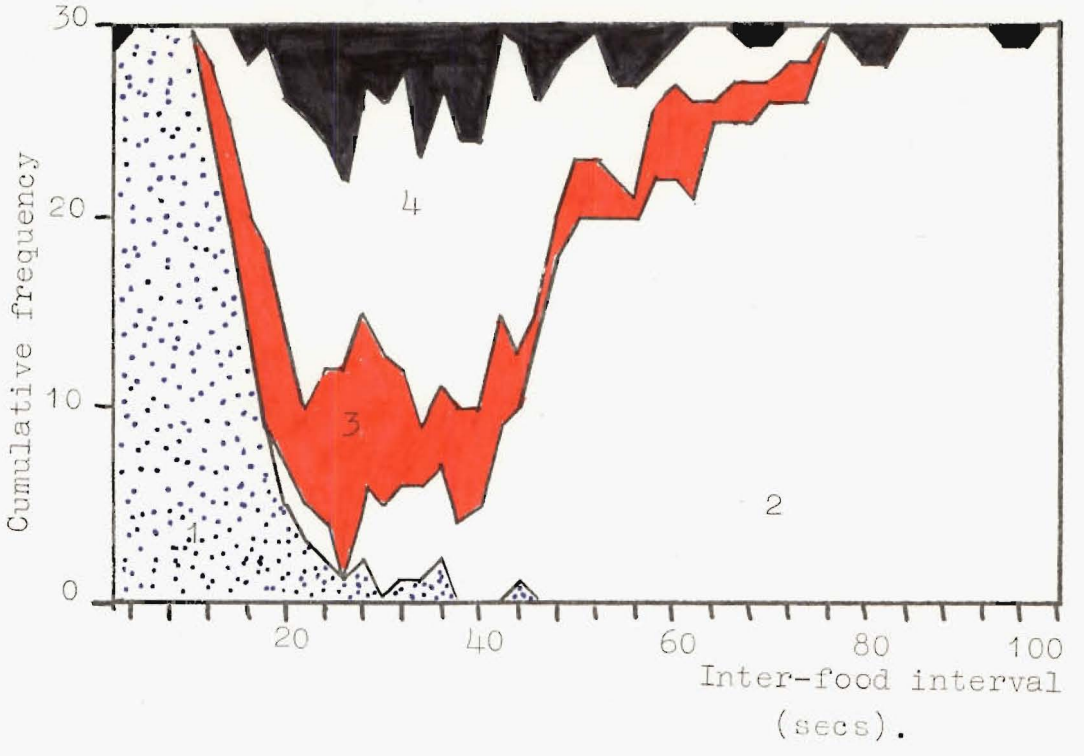


Figure 6:6 (d) Subject F2.



availability of food. The other categories of behaviour also show a relatively stable pattern, with S, Sct and M showing little variation across the different sessions. Scb shows the influence of individual differences (F2 engaging in this behaviour more than F1). The combined stationary categories of Hi and I occur at a high level (of the order of 35 - 50% of all observations), although some individual differences appear. Significantly Hi is a frequent behaviour in both animals, showing that these animals spent much of the time resting with their heads in the food receptacle (as is shown in the following section dealing with the temporal distributions of the various overall categories). The category M reflects the great range of low frequency behaviours in ferrets (up to 13% on one occasion) compared with the rats (where this category never exceeded 2% of the observations). This high occurrence of category M in ferrets may be partially attributable to the greater range of behaviours that ferrets demonstrated in the experimental situation, and partially to the difficulties experienced in categorizing and recording their behaviour.

(b) The cumulative temporal distributions of overall categories. The patterns of behaviour shown in Figures 6:5 a-d and 6:6 a-d reveal several different features to those of the rats.

Category 1 - *(immediate food-oriented behaviour)* shows a similar pattern to the rats, with the ferrets rapidly learning the temporal probability of food delivery. This pattern is predictable, since the occurrence of this category of behaviour must directly relate to the delivery

of food in food deprived animals..

Category 2 - (*stationary behaviours*) differs from that of the rats in that grooming does not contribute to this category in ferrets (in all, no more than a total of 60 observations of grooming were ever observed in the ferrets over all sessions). Category 2 in ferrets was comprised of protracted bouts of immobile behaviour, and was the most frequently recorded overall category in both subjects. Furthermore, this behaviour increased in frequency over the inter-food interval, and reached a probability of near unity in the last quarter. Instead of grooming, sniffing or ambulating in the latter portions of the interval (the pattern observed in rats), the ferrets simply lay down until the next food portion was delivered.

Categories 3 - (*Sniffing*), 4 (*Scratching behaviour*) and 5 (*miscellaneous*) all show a similar temporal distribution, and can be considered together. These categories appear with an approximately equal probability in the interval immediately following category 1 (*immediate food-oriented behaviours*) and show a decline across the inter-food interval as the probability of Category 2 (*stationary behaviours*) increases. At the point of their maximum probability of occurrence these categories occupy the position where schedule-induced polydipsia occurs in rats. Thus the difference between the rats and ferrets in this portion of the interval is expressed as one behaviour becoming predominant (polydipsia) in the rats, and several behaviours occurring without one predominating in the ferrets.

In general the temporal distributions of the various behaviours between the two species show a different pattern after the food is delivered and consumed. In the rats, a limited range of behaviours occurs, until the latter positions of the interval where categories 2 and 4 occur with approximate equal probability. In the ferrets the post-food interval is characterised by the occurrence of a range of behaviours, with their rapid diminuition as the animals developed one exclusive pattern towards the end of the interval (i.e. immobile waiting). Whereas the rats developed polydipsia, the ferrets did not direct their behaviour to one specific aspect of their experimental environment. This suggests that either there is a phylogenetic/ecological factor operating in ferrets to prevent their attending to a limited range of behaviours in this situation, or that the experimental situation did not provide these animals with an appropriate object to direct appropriate behaviours towards. This suggestion is further considered in the next section.

(E) General Discussion.

The results from the observational study are important in that they illuminate the patterns of behaviour of the respective species in the experimental situation. The development of schedule-induced polydipsia in the rats, occuring in the period following eating, increases in magnitude over successive sessions to the exclusion of most other behaviours. In the latter portions of the inter-food interval the polydipsic behaviour declines,

and the rats engage in either *stationary behaviours* (grooming and sitting still)or *active investigatory behaviours* (ambulation, rearing and sniffing).

The interval following the delivery and consumption of food in ferrets is characterised by the occurrence of a variety of behaviours, none of which develops to the exclusion of all others. This suggests that a process of behavioural variation is operating in this portion of the interval. Towards the latter portions of the inter-food interval the ferrets developed a pattern of immobile behaviour, remaining so until the next food delivery. This behaviour rapidly developed to the virtual exclusion of all other behaviours (in a manner akin to the development of polydipsia in rats, although later in the interval).

These results relate closely to the species-generality of adjunctive drinking, as they show that the rat directs its behaviour towards the drinking tube when feeding is delayed, whereas the ferret exhibited a pattern of variability without any one behaviour predominating. In terms of Staddon and Simmelhag's model (and that of Garcia *et al*) the drinking in rats and the variable behaviours in ferrets occurred in the period associated with interim activities, as predicted in section c (4).

It may be speculated that these differences in the interim activities reflect ecological features of these respective species , the rat persevering with a limited range of behaviours (in keeping with its natural pattern of sustained food seeking), while the ferret engaged in a range of behaviours (as might be expected of a species that has to "start over again" should it miss it's prey

at the first attempt at capture).

The behaviours exhibited in the latter portion of the inter-food interval also suggest a strong ecological/phylogenetic influence. The rats engaged in *stationary behaviours* and *active investigatory behaviours* to an equal extent, except when the drinking tube was removed, and then a marked increase in grooming and "freezing" occurred (implying some sort of mediating behaviours were predominating). The ferrets were almost exclusively engaged in protracted bouts of remaining immobile, usually with their heads resting in the food hopper. This pattern of quiescence has been noted elsewhere in the cat. Since these two species both share the carnivorous mode of living, it is reasonable to assume that some common features exist between the cat's behaviour and that of the ferret. Breland and Breland (1966) note that cats often become immobile if a delay in food delivery is imposed upon them in the laboratory setting: [4]

> "Also, because the cat does not course his game, his persistence for food at any one time is not too long-lived. If we require the cat to make a response requiring a larger outlay of energy, he will go through one sequence but then may very well lie down and go to sleep if he doesn't achieve success in the first trial". (p. 90).

4. Their behaviour in the laboratory situation usually involves a strong learned component as to when feeding occurs, as opposed to the behaviour in the wild where feeding is related to availability of prey etc.

This pattern of sleeping in cats, in situations involving "thwarting" or "frustration" of consummatory behaviour, has been considered as a form of displacement behaviour of this species.

> "In the cat, Parmeggiani stimulated several different and separate areas of the forebrain and brainstem and obtained a behavioural complex consisting of sniffing, grooming, lying down, curling up, dozing and sleeping. He emphasizes that this behaviour is normal in unstimulated cats ..... Again, Leyhausen lists grooming, sniffing and lying down as displacement behaviour for the cat". (Delius, 1967).

In his consideration of displacement sleeping in cats, Delius notes that the situations that produce displacement behaviour involve an increase in arousal (i.e. as a result of thwarting, frustration and conflict). He sees sleep (and other displacement behaviours such as grooming and lying down) as part of a homeostatic de-arousal process:

> "I suggest that the occurrence of at least some displacement activities is the reflection of a homeostatic process operating towards cancelling the arousal increment so generated, through the activation of an arousal inhibiting system ..... The striking occurrence

of sleep as displacement in several species may be regarded as a regulatory overshoot".

From this statement (and the Brelands' observations) it may be concluded that, a situation known to produce displacement sleeping and lying down in cats, also appears to produce quiescent behaviour in another carnivore, the ferret. As was discussed in section C (4), displacement and adjunctive behaviours appear to be functionally, causally and adaptively similar, and so the long bouts of immobility observed in the ferrets may reflect a tendency amongst some carnivores to remain still when the chances of eating are slight.

That these periods of immobility in ferrets occur in the latter portions of the inter-food interval, after a period of behavioural variability suggests that there are strong ecological and phylogenetic factors being induced in the experimental situation. Although immobility occurred to the exclusion of most other behaviours, it is difficult to consider it as an adjunctive behaviour, according to the usual description of phenomenon. Firstly, the periods of immobility were inevitably restricted to the latter portions of the inter-food interval (instead of the immediate post-food interval where adjunctive behaviours are usually observed). Secondly, unlike schedule-induced polydipsia that initially occurred at a low level and increased to a high level (from approximately 10% to 35% of all observations), immobility initially occurred at a high level and increased in magnitude to a comparatively lesser extent (from approximately 40% to 50% of all

observations). Thus immobility differs from schedule-induced polydipsia in both the temporal locus and in that it does not develop over successive sessions. The behaviour of the rats did not reflect this pattern; rather a series of different behaviours emerged, demonstrating that the rats remained active throughout the inter-food interval as might be expected of a small omnivore that has to contend with regular bouts of eating and many predators.

That species-typical behaviours occur in a situation involving an intermittence of food availability in food deprived animals is not unexpected, as Falk (1977) has succinctly stated:

> "As noted, displacement behaviours are under the control of facilitating stimuli and thus not entirely incongrous with respect to situational vectors. Likewise, adjunctive behaviours are not newly engendered activities. They are increased in the magnitude and probability of behaviours *already present as moderate base-rate responses to the general situation.* (Falk, 1971). Both displacement and adjunctive activities probably are produced by much the same stimuli that produce these behaviours (drinking, aggression, nest-building etc.) in other, more usual situations. The unusual features involve the temporal locus of such behaviour and its apparently nonfunctional exaggeration". (Italics mine).

A question remains as to why no defined adjunctive behaviours were observed in ferrets (compared with the excessive drinking in rats). Although several behaviours were observed in the immediate post-food interval (i.e. the period of interim activities) none developed to the exclusion of others. Two possibilities may account for this.

Firstly, an appropriate stimulus may not have been present to serve as a focal point for any potential adjunctive behaviour; although two manipulations that produce adjunctive behaviour in other species (drinking and wheelrunning) did not lead to increased behaviour in ferrets. Possibly, schedule-induced aggression might be a suitable behaviour to examine in this respect, although seasonal, social, and learning variables are involved in this particular behaviour in ferrets (and would require both extensive investigation and control).

Secondly, ferrets may not be prone to development of adjunctive behaviours. This possibility relates back to Falk's (1977) prediction, as discussed in the introduction of Chapter 5, in which he suggested that "the very mobile hunters with large prey-search times relative to prey-pursuit times", with "low patch-fugacity thresholds" should yield food-schedule-induced adjunctive behaviours most readily". Assuming that ferrets are indeed very mobile hunters that fit the patterns described by Falk, then this prediction has not been borne out in the present experiments. However, it may also be possible that ferrets are animals which exhibit a "less mobile mode of foraging", for which Falk predicts "less adjunctive behaviour, but it may not be

inconsequential". In the absence of firm observational data of the natural modes of foraging in ferrets, the assigning of these categories can only remain speculative. The only firm conclusion that may be drawn is that under the experimental conditions imposed upon the ferrets in this study they did not develop schedule-induced polydipsia or schedule-induced wheel running, whereas rats did develop polydipsia.

C H A P T E R S E V E N

DISCUSSION AND CONCLUSIONS.

(A) The Durability of Schedule-Induced Polydipsia.

The experimental manipulations necessary to produce schedule-induced polydipsia in rats are few and simple. The research reported herein has repeatedly demonstrated the simplicity of induction, and the magnitude of this phenomenon. Every rat developed polydipsic responding within six to eight sessions, and all consumed water markedly in excess of their normal daily home cage level in the space of approximately two and three quarter hours.

Despite the ease with which schedule-induced polydipsia can be demonstrated, a review of the literature and the experiments discussed in the earlier chapters, reveal that no simple explanation for this phenomenon exists. Rather, the nature of the variables influencing schedule-induced polydipsia, and the relationship between this phenomenon and other behaviours (e.g. displacement activities and interim activities), suggest that a complex interaction between exogenous and endogenous stimuli, motivational systems, and phylogenetic factors are involved.

Beyond demonstrating schedule-induced polydipsia in every subject tested, the procedure used in the present research confirms previous findings that response-contingency is not necessary for the induction of this behaviour.

The simplified procedure, without the familiar lever of operant research, and without retractable drinking tubes produced reliable polydipsia and permitted an investigation of the temporal locus of this behaviour in a satisfactory manner. The simplicity of this manipulation raises a question as to the necessity to use bar-pressing (itself a potential adjunctive behaviour; Wayner and Greenberg, 1973), and retractable water sources (Flory and O'Boyle, 1972; Gilbert, 1974) when these items are potential sources of confounding the results (through acquiring the properties of discriminative stimuli themselves, as noted in Chapter 4).

The levels of polydipsia obtained in this research were not as high as observed by other researchers (e.g. Falk reports increases of the order of 300%-400% in many cases) but this may be a consequence of the type of food pellet used. As noted in Chapter 2, the presence of sugar in the pellets reduces fluid intakes relative to the intakes obtained with sugar-free pellets (Christian and Schaeffer, 1973a, 1973b). The pellets used in this research contained 11% dextrose by weight, and this may have contributed to the lowered levels of polydipsia, although it was felt that these particular pellets had the benefit of standardised size and content, compared to wheat (used in the pilot study).

In general the features and development of schedule-induced polydipsia observed in this research, confirms Falk's 1972 observation that:

> "The conditions that produce schedule-induced polydipsia are not complex. The experimental design is simple, yet the behavioural effect is strong and durable".

(B) The Temporal Locus of Schedule-Induced Polydipsia.

The results reported in Chapters 4 and 6 confirm that under the procedure used, schedule-induced polysipsia is predominantly an immediate post-pellet phenomenon, as suggested by Falk (1969), although not exclusively so, as some responding does occur throughout the latter portions of the inter-food interval.

These results suggest some consideration of methodological factors is necessary in studies that purport to examine the temporal distribution of polydipsia. Firstly, as has been discussed above, the use of the bar-press response (and of retractable levers etc.) is a possible source of confounded results. Secondly, these responses must also have an influence on the temporal locus of polydipsia as a consequence of simple logistics, since the animal has to perform a number of responses first before drinking. A good example of this is Killeen's (1975) studies on the temporal locus of polydipsia, in which he sought to,

> "determine whether the time course of schedule-induced polydipsia corresponds to that of the interim and terminal behaviours ....."

In his experiment, water was obtained via a bar-press on a CRF schedule, and the rate of responding on this lever was included in the analysis of the data based upon a mathematical model of temporal responding. He concluded that,

> "Schedule-induced polydipsia is often characterized as a "post-pellet phenomenon". The present experiments belie that description and show that, while there is some post-pellet drinking, the maximum rate of drinking occurs half-way through the interpellet interval".

Despite the elegance of the data analysis, this conclusion is questionable on the grounds that the animal's drinking was made more effortful because of the bar-press contingency, and this may have served to extend the drinking further into the inter-pellet interval. It is not clear why Killeen used a bar-press measure of response rate, when a simple drinkometer could provide the same data without resort to increasing the complexity of the experimental situation.

Beyond methodological questions, the data from the present experiments indicate that schedule-induced polydipsia occurs predominantly in that interval where interim activities have been described, and thus confirm the relationship between adjunctive behaviours and interim activities. This relationship is most evident from the observational studies reported in Chapter 6, on the polydipsic behaviour of rats, and suggests that Staddon and Simmelhag's model has considerable application to these

findings.

(C) Schedule-Induced Licking Behaviour.

As discussed in Chapter 4, the finding that rats would respond at a high rate to a licking tube without drinking being possible was both unexpected, and not clearly understood. The responding to the licking tube was often indistinguishable from that recorded on the drinking tube (i.e. polydipsia) in terms of magnitude of licking and temporal distribution. However, individual differences were greater with schedule-induced licking.

The extent of individual differences in schedule-induced licking, and the fact that the choice experiments show a clear preference for polydipsia, suggests that licking may be a subsidiary response to drinking. This possibility also draws support from Segal's (1973 , pers. comm.) suggestion that two separate but related topographies may be induced. If the licking response was a subsidiary component of drinking behaviour, it may be speculated that some innate hierarchical organisation of these behaviours is being invoked when an animal is put in the usual experimental situation. Support for such a view may be drawn from the research on stimulus-bound behaviour (e.g. Valenstein, Cox, and Kakolewski; 1969, 1970), in which these authors discussed the results of electrical brain stimulation studies, finding:

> "Hypothalamic stimulation does not activate only one specific behaviour pattern. The stimulation seems to

> excite the substrate for a group of responses that in a given species are related to a common state". (Valenstein *et al*, 1970; cited in Staddon and Simmelhag).

Further support for such a hierarchial system may be drawn from the ethological research on "disinhibition" in displacement behaviour (e.g. Andrew, 1956; McFarland, 1966). This view is well summarised by Hinde (1966):

> "when mutual incompatibility prevents the appearance of those types of behaviour which would otherwise have the highest priority, patterns which would otherwise have been suppressed are permitted to appear".

Staddon and Simmelhag note that this view has relevance both to interim activities and adjunctive behaviour.

Beyond consideration of possible explanations for schedule-induced licking behaviour is a more immediate issue of why licking occurred at such a sustained level in the present experiments, when other researchers report neglible licking when water is not available (e.g. Stein, 1964). Although Cook and Singer (1976) reported some licking when the drinking tube was emptied, the levels obtained were markedly less than comparable levels when these subjects were polydipsic. The present data show licking behaviour and polydipsia to be frequently indistinguishable in terms of licks recorded and the temporal distribution of responding. Control sessions data tended to rule out

rewarding drinkometer current effects (as suggested by Cook and Singer) since the animals continued to lick at the tube even after 6 days of the drinkometer being disconnected. Another possibility, schedule-induced tongue-cooling effects (Mendelson and Chillag, 1970) cannot be discounted, although the magnitude of licking tube effects seems too large to be accounted for by this factor alone.

Clearly schedule-induced licking behaviour requires further empirical investigation to determine what the causal factors are, as this question cannot be determined by the present data. However, these findings do suggest a strong influence of oral features in this behaviour, and possibly in schedule-induced polydipsia.

(D) The Species-Generality of Schedule-Induced Polydipsia.

The failure to demonstrate schedule-induced polydipsia in ferrets joins the findings from guinea pigs (Freed, Zec and Mendelson, 1977), golden hamsters (Wilson and Spencer, 1975), and pigeons (Whalen and Wilkie,1977) as species that do not exhibit this behaviour under conditions that produce it in rats and rhesus monkeys. These results add weight to Wilson and Spencer's suggestion that,

> "more comparative research is needed if the underlying determinants of schedule-induced polydipsia are to be discovered".

However, there is an implicit danger in a comparative examination of schedule-induced polydipsia, and this relates to a point that Hodos and Campbell (1969) have raised regarding the reasons for using the comparative method of study. They note that much comparative research appears to be based upon comparisons between species,

> "that have been selected for study according to rather arbitrary considerations....." [1]

Accordingly, the basis by which various species are selected for a comparative investigation of schedule-induced polydipsia is important, as consideration of the animal's mode of living may determine its suitability for such investigations. It may be speculated that desert-dwelling animals would not develop polydipsia because of the way in which their physiological systems are adapted to the conservation of liquids, and that the browsing ungulates of the African savannah (e.g. eland, antelopes, zebra etc) also might not show this behaviour because of their adaptation to infrequent drinking in this drought-ridden niche.

The choice of the ferret as a suitable subject can be justified on the basis of Falk's prediction (as noted in Chapter 5) regarding the propensity to adjunctive behaviour of different species from various ecological niches.

1. For an expanded discussion of this issue see page 14 of Appendix 1.

Without the comparative observational study reported in Chapter 6, the results from Chapter 5 might appear somewhat trivial, since they would not have shown the variable behaviour after eating and the long bouts of immobility before food delivery.

Ecological factors may be significant determinants of whether schedule-induced polydispsia occurs, and whether other adjunctive behaviours develop, as is recognised by Falk (1977). It would seem that the close relationship between eating and drinking in the rat has a major bearing on polydipsia being a highly probable adjunctive behaviour. In this species, and presumably in other species, the likely form of any adjunctive behaviour must relate closely to the "natural" (i.e. innate) organisation of behaviour. This point is recognised by Falk (1977) when he states that,

> "adjunctive behaviours are not newly engendered activities. They are increases in the magnitude and probability of behaviours already present as moderate, base-rate responses to the general situation".

This comment leads to a consideration of the adaptive features of adjunctive behaviours, since at the initial level schedule-induced polydipsia appears both maladaptive and toxic to the well-being of the animal. However, as discussed in Chapter 4 (p. 24), Falk has emphasised that the "environmental circumstances - the ecology of the situation" has an important bearing on whether adjunctive behaviour can be considered as a creative or toxic

response. Thus schedule-induced polydipsia may be considered, not as a pathological propensity in rats to over indulge in drinking, but as a peculiar property of the unnatural experimental situation that the laboratory specimen is placed in. Because of the features of the experimental situation, a normally adaptive behaviour becomes exaggerated and apparently nonfunctional. Yet the underlying mechanism, in the "natural" environment has an advantage to the animal in that it stabilizes a number of activities in situations of moment to moment instability, as Falk (1977) has described:

> "Thus, adjunctive behaviour can either stabilize pre-existing, adaptive behaviour in an otherwise unstable situation or be so invasive in vulnerable situations that it eliminates other species of behaviour. Whether this latter outcome is creative or toxic for the organism depends upon the overall adjustive value of the newly dominant behaviour".

As adjunctive behaviours appear to have an adaptive value to the organism, and are related to displacement behaviours then they conform to the evolutionary principles governing life in a changing environment. It is to this adaptive value that consideration of the species-generality of adjunctive behaviours needs direction.

> "The reinforcement intermittence and thwarting conditions that yield adjunctive and displacement behaviours increase the organism's probability of

> responding in strength to other possibilities in the environmental context by increasing the gain on operant units receiving relatively low, but appreciable, facilitation from current environmental stimuli. In this regard, Armstrong (1950) comments that 'a species which is able to modify its behaviour to suit changed circumstances by means of displacement, rather than by the evolution of *ad hoc* modifications starting from scratch, will have an advantage over other species. Therefore, *ceteris paribus*, a displacement-prone species will be more adaptable, and consequently more successful, than a species not so equipped'. But he also ironically observes: 'No doubt many dysgenic displacements have been eliminated with their performers in the course of evolution'". (Falk, 1972).

(E) Suggestions for Further Research.

The technique adopted to investigate the temporal distribution of schedule-induced polydipsia in rats was both simple and effective. The main difficulty encountered in this experimentation related to the transcription of drinkometer records onto data sheets, a process that would

be greatly facillitated if an array of counters were used to record the actual number of licks in each successive 'bin'. This modification would have an advantage beyond making the recording easier, as the overall technique could be applied to assessing the effects of various pharmacological agents on the general behaviour of an animal.

Schedule-induced polydipsia has been used to obtain high levels of alcohol ingestion in rats (indeed the second publication describing this phenomenon used a 5.6% (w/v) solution of ethanol, see Lester, 1961) and the high levels of self-intoxication obtained in rats by this procedure are unique in many respects. Not only do the animals ingest alcohol "somewhat voluntarily", but after sustained consumption of ethanol by this procedure they appear to develop withdrawal symptoms when access to it is denied. (Hawkins, Schrot, Githens and Everett, 1972; Falk, Samson and Winger, 1972).
The significance of these findings is noted by Hawkins *et al*, who comment,

> "To our knowledge, no similar observations of possible alcohol deprivation effects in rodents have been reported. This is substantiated in a recent review by Mello (1968). There have been only a few suggestions that alcohol deprivation has produced demonstrable behavioural or physiological changes in any animals other than man..... Our observations are only a tiny suggestion that it is

possible to produce physical dependence in rats, but these results are extremely encouraging".

An analysis of the temporal distribution of schedule-induced alcohol consumption over time may reveal both the effects of intoxication, and the physiological impairment due to this ingestion.

Beyond investigating the effects of alcohol, the effects of known dosages of various pharmocological agents on the nervous system might be investigated through an analysis of the temporal distribution of polydipsia. Of empirical interest is the sensitivity of the temporal distribution of this behaviour to various factors that change the internal state of an animal. If this measure is found to be sensitive it may have an advantage over various other measures that use learned responses (i.e. bar-press, key pecks e.t.c.).

In considering a further investigation of adjunctive behaviours in ferrets, a number of empirical directions are suggested. The occurrence of manipulative behaviours in this species (e.g. scratching and scrabbling) suggests that some sort of manipulandum could be provided in the experimental situation towards which these activities could be directed. An auditory attachment to such a device (perhaps a simple ratchet) might be required in order to give some sensory feedback to the subjects. Another variable that might be manipulated is the palatability of the liquid provided in a potential polydipsic situation, although the present data suggest polydipsia is a very unlikely behaviour in this species.

An alternative approach to investigating the behaviour of ferrets would entail making the experimental environment more complex,[2] through the provision of several recesses, objects to climb on, and numerous movable objects to manipulate, in order to see whether the natural playfulness and curiosity observed in the home-cages (the "destructive ingenuity" described in Chapter 5 regarding the development of the activity wheel) might prevail over the tendency to remain immobile. In this situation an observational analysis of the animals may also give some indication of the extent to which the lack of complexity in the usual experimental environment influences the patterns of behaviour.

The results of the observational study, while demonstrating some aspects of the behaviour of ferrets, requires extending to examine changes in the inter-food interval, as this variable is known to have importance to the behaviour of rats (e.g. Falk, 1966b; Hawkins, Schrot, Githens and Everett, 1972). Also, a parametric investigation of the size of food portions is desirable, as this is also a significant variable in the behaviour of rats (e.g. Falk, 1969). It may be speculated that, small food portions that are made available on an intermittent basis, may not have the same importance to a species that normally acquires its total meal in one sequence of behaviour (i.e. a carnivore) compared with an omnivore (that is adapted to sustained food-seeking behaviour consequential to its ecological niche).

2. A similar consideration also applies to rats.

Finally, in testing Falk's (1977) prediction regarding the propensity to food-schedule-induced adjunctive behaviours in carnivores, the ferret may not be an entirely appropriate subject. Although ferrets are carnivores, the evidence presented in Appendix Two suggests that this species does not make extensive use of visual cues when hunting in the natural state. The role of smell in prey-searching is great in this species, and this may have considerable bearing on the results obtained in the present research. It may be more advisable to use the domestic cat as a subject, since this species is more visual, and can be considered a very mobile hunter. Also, unlike the ferret, a substantial body of research has been accumulated on the behaviour of cats, and this may be of assistance in understanding the experimental data obtained.

(F) In Conclusion.

A number of conclusions can be drawn from the research reported in this thesis. Investigations of the temporal locus of schedule-induced polydipsia in rats reveal that this behaviour is predominantly a post-pellet phenomenon, although not exclusively so, as some minimal drinking does occur in the latter segments of the inter-food interval. Furthermore, this finding has been achieved with an essentially simple experimental paradigm, and circumvents many methodological difficulties of other techniques that have examined this question. Additionally, an unexpected discovery was made, that the subjects continued to respond at an equivalent level to a tube which did not permit

drinking to occur. This finding is contrary to expectation. The similarity between the magnitude and temporal distribution of responding on both the drinking and licking tubes suggests that a closely related phenomenon was being induced in both situations. Although schedule-induced licking was not fully investigated, the present data suggest that this phenomenon could be a subsidiary response of drinking which is denied full expression by the particular nature of the licking tube.

The results from both schedule-induced polydipsia and licking suggest that these behaviours are highly prepotent in the rat, as is indicated by the vigour with which they develop. This implies the influence of some innate organisation of these behaviours in this species. Further evidence for this view can be drawn from the behaviour of the ferrets, where attempts to induce schedule-induced polydipsia were met with failure.

Despite these negative results from ferrets, an observational study revealed that the behaviour of this species has a definite organisation, with a number of species-typical behaviours in evidence. Where rats directed their attention to drinking, ferrets engaged in a range of behaviours. These findings have a great importance to any explanation for schedule-induced polydipsia (and adjunctive behaviours generally).

The demonstration of a limited species-generality must crucially influence any theoretical account of this phenomenon, since many explanations have been couched in a "general process" framework. Such approaches are clearly invalid, since they are unable to account for the limited

generality of this behaviour. In fact, despite extensive theorising, schedule-induced polydipsia has only ever been reliably produced in rats and certain species of monkeys.

This observation, and the present results, lead to an unavoidable conclusion: any theoretical explanation for schedule-induced polydipsia must necessarily account for the limited species-generality of this phenomenon, or else be labelled as 'yet another theory' of rat behaviour.

The overdependance upon the rat has been a frequently cited criticism of experimental psychology. The present results support such a criticism, as the data only become understandable when considered in conjunction with the natural behaviour of the two species studied.

When viewed from the perspective of the variability, and adaptiveness of behaviour, these differences between rats and ferrets serve to emphasize the need to relate laboratory-based procedures to the natural, evolutionary and ecological origins of animal behaviour.
As is discussed in an essay in Appendix One, the various approaches to the study of animal behaviour have often pursued courses that have frequently been characterised by acrimony and polemics with little interchange between the fruitful spirits of each viewpoint. The current state of harmonious interchange between these approaches is both laudable and necessary if the advancement of the science of animal behaviour is to succeed. This view has often been stated; but perhaps most clearly by Daniel Lehrman, in a volume dedicated to the memory of T.C. Schneirla,

and which may serve as an epilogue.

E P I L O G U E.

Semantics, Concepts, and Facts.

When opposing groups of intelligent, highly educated competent scientists continue over many years to disagree, and even to wrangle bitterly, about an issue they regard as important, it must sooner or later become obvious that the disagreement is not a factual one, and that it cannot be resolved by calling to the attention of the members of one group (or even of the other!) the existence of new data which will make them see the light. Further, it becomes increasingly obvious that there are no possible crucial experiments that would cause one group of antagonists to abandon their point of view in favour of that of the other group. If this is, as I believe, the case, we ought to consider the roles played in this disagreement by semantic difficulties arising from concealed differences in the way different people use the same words, or in the way the same people use the same words at different times; by differences in the concepts used by different workers (i.e., in the ways in which they divide up facts into categories); and by differences in their conception of what is an important problem and what is a trivial one, or rather what is an interesting problem and what is an uninteresting one.

(Lehrman, 1970).

R E F E R E N C E S

ADOLPH, E.F. (1947) Urges to eat and drink in rats. Amer. J. Physiol., 151, 110-125.

ALTMANN, J. (1974) Observational study of behaviour: sampling methods. Behav., 49, 227 - 267.

ANDERSON, M. (1974) Temporal graphical analysis of behaviour sequences. Behav., 51, 38-40.

ANDREW, R.J. (1956) Some remarks on behaviour in conflict situations with special reference to Emberiza spp. Brit. J. Anim. Behav., 4, 41-45.

ARMSTRONG, E.A. (1947) Bird display and behaviour. London: Cambridge Univ. Press.

ARMSTRONG, E.A. (1950) The nature and function of displacement activities. Symp. Soc. Exp. Biol., 4, 361-386.

AZRIN, N.H. (1966) HUTCHINSON, R.R., and HAKE, D.F. Extinction-induced aggression. J. Exp. Anal. Behav., 9, 191-204.

BASTOCK, M., MORRIS, D., and MOYNIHAN, M. (1953) Some comments on conflict and thwarting in animals. Behav., 6, 66-84.

BAUM, M. (1970) Extinction of avoidance responding through response prevention (flooding). Psychol. Bull., 74, 276 -284.

BEACH, F.A. (1950) The snark was a boojum. Amer. Psychol., 5, 115-124.

BERLYNE, D.E. (1960) Conflict, arousal and curiosity N.Y: McGraw-Hill.

BINDRA, D. (1959) An interpretation of the "displacement" phenomenon. Brit. J. Psychol., 50, 263-268.

BINDRA, D. (1969) The interrelated mechanisms of reinforcement and motivation, and the nature of their influence on response. Nebraska Symp. Motiv., 17, 1-37.

BINDRA, D., and BLOND, J. (1958) A time-sample method for measuring general activity and its components. Canad. J. Psychol., 12, 74-76.

BINDRA, D., and SPINNER, N. (1958) Response to different degres of novelty: the incidence of various activities. J. Exp. Anal. Behav., 1 341 - 350.

BOLLES, R.C. (1961) The interaction of hunger and thirst in the rat. J. Comp. Physiol. Psychol., 54, p 580-584.

BOLLES, R.C. (1967) Theory of motivation. N.Y: Harper and Row.

BOLLES, R.C. (1970) Species-specific defense reactions and avoidance learning. Psychol Rev., 77, 32-48.

BRELAND, K. and BRELAND, M. (1951) A field of applied animal psychology. Amer. Psychol., 6, 202-204.

BRELAND, K., and BRELAND, M. (1961) The misbehaviour of organisms. Amer. Psychol., 16, 681-684.

BRELAND, K. and BRELAND, M. (1966) Animal behaviour. 1966 Macmillan: N.Y.

BROWN, P.L., and JENKINS, H.M. (1968) Auto-shaping of the pigeon'n key-peck. J. Exp. Anal. Behav., 11, 1-8.

BURKES, C.D., HITZING, E.W. and SCHAEFFER, R.W. (1967) Drinking response distributions assiciated with a 4 percent sucrose FFI food schedule. Psychon. Scie., 8, 13-14.

CANNON, W.B. (1918) The physiological basis of thirst. Proc. Roy. Soc. Lond., 90b, 283-301.

CHRISTIAN, W.P., and SCHAEFFER, R.W. (1973a) Note: advisability of using sugar-free food pellets for schedule-induced polydipsia research. Psychol. Rep., 32, 274.

CHRISTIAN, W.P., and SCHAEFFER, R.W. (1973b) Effects of sucrose concentrations upon schedule-induced polydipsia on a FFI-60-sec dry-food reinforcement schedule. Psychol. Rep., 32, 1067-1073.

CLARK, F.C. (1962) Some observations on the adventitious reinforcement of drinking under food reinforcement. J. Exp. Anal. Behav., 5, 61-63.

COOK, P., and SINGER, G. (1976) Effects of stimulus displacement on an adjunctive behaviour. Physiol. and Behav., 16, 79-92.

DALE, R. (1975) Schedule-induced drinking in the pigeon: its temporal location and influences on operant key pecking. Unpunl. Masters thesis, Dalhousie Univ. (cited by Whalen and Wilkie, 1977).

DELIUS, J.D. (1967) Displacement activities and arousal. Nature, 214, 1259-1260.

DELIUS, J.D. (1969) A stochastic analysis of maintenance behaviour of skylarks. Behav., 33, 137-171.

DUFFY, E. (1962) Activation and behaviour. N.Y: Wiley.

ESTES, W.K. (1959) The statistical approach to learning theory. In: KOCH, S (ed). Psychology - a study of a science Vol 2. N.Y: McGraw-Hill.

FALK, J.L. (1961a) Production of polydipsia in normal rats by an intermittent food schedule. Scie., 133, 195-196.

FALK, J.L. (1961b) The behavioural regulation of water- and electrolyte balance. in: Nebraska Symp. Motiv., 1961, Lincoln, Neb: Univ. Neb. Press. 1-33.

FALK, J.L. (1964) Studies on schedule-induced polydipsia. in: Wayner, M.J. (ed). Thirst: first international symposium on thirst in the regulation of body water. N.Y: Pergamon Press. 95-116.

FALK, J.L. (1966a) The motivational properties of schedule-induced polydipsia. J. Exp. Anal. Behav., 9, 19-25.

FALK, J.L. (1966b) Schedule-induced polydipsia as a function of fixed-interval length. J. Exp. Anal. Behav., 9, 37-39.

FALK, J.L. (1967) Control of schedule-induced polydipsia: type, size and spacing of meals. J. Exp. Anal. Behav., 10, 199-206.

FALK, J.L. (1969) Conditions producing psychogenic polydipsia in animals. Annals N.Y. Acad. Scie., 157, 569-593.

FALK, J.L. (1971) The nature and determinants of adjunctive behaviour. Physiol. and Behav., 6, 577-588.

FALK, J.L. (1972) The nature and determinants of adjunctive behaviour. In: GILBERT, R.M. and KEEHN, J.D. (eds) Schedule effects: drugs, drinking and aggression. Toronto and Buffalo: Univ Toronto Press.

FALK, J.L. (1977) The origin and functions of adjunctive behaviour. Anim. Learn. Behav., 5, 325-335.

FALK, J.L., SAMSON, H.H., and WINGER, G. (1972) Behavioural maintenance of high concentrations of blood ethanol and physical dependence in the rat. Scie., 177, 811-813.

FLORY, R.K. (1969c) The control of schedule-induced polydipsia: frequency and magnitude of reinforcement. Unpublished Ph.D. dissetation, Arizona state Univ., 1969.
(cited in Falk, 1972).

FLORY, R.K. and O'BOYLE, M.K. (1972) The effect of limited water availability on schedule-induced polydipsia. Physiol. and Behav., 8, 147-149.

FRASER, D. (1976) Unpubl. Manuscript, Dalhousie Univ.
(cited in Whalen and Wilkie, 1977).

FREED, E.X. (1971) Schedule-induced polydipsia with nutritive and nonnutritive reinforcers. Psychon. Scie., 23, 367-368.

FREED, W.J., ZEC, R.F., and MENDELSON, J. (1977) Schedule-induced polydipsia: the role or orolingual factors and a new hypothesis. in: Weijnen, J.A.W.M. and Mendelson, J. (eds). Drinking Behaviour. N.Y: Plenum. (in press) cited in Porter, Zec, and Mendelson (1977).

FREUD, S. (1915) Instincts and their vicissitudes. in: Collected papers IV. N.Y: Basic Books. (1959).

GARCIA, J. and KIMELDORF, D.J. (1960) Some factors which influence radiation-conditioned behaviour in rats. Radiation Research., 12, 719-722.

GARCIA, J., KIMELDORF, D.J., and HUNT, E.L. (1961) The use of ionising radiation as a motivating stimulus. Psychol. Rev., 68, 383-395.

GARCIA, J., CLARKE, J.C., and HANKINS, W.G. (1973) Natural responses to scheduled rewards. In: Bateson, P.G.G., and Kloper, P.H. (eds) Perspectives in ethology. N.Y., London: Plenum.

GHISELIN, M.T. (1973) Darwin and evolutionary psychology. Science., 179, 964-968.

GILBERT, R.M. (1974) Ubiquity of schedule-induced polydipsia. J. Exp. Anal. Behav., 21, 277-284.

GLICKMAN, S.E. (1973) Responses and reinforcement. In: Hinde, R.A., and Stevenson-Hinde, J. (eds) Constraints on learning: limitations and predispositions. London, N.Y: Academic Press.

GLICKMAN, S.E. and SCHIFF, B.B. (1967) A biological theory of reinforcement. Psychol. Rev. 74, 81-109.

HAWKINS, T.D. (1967) Pellet frequency: effects on schedule-induced polydipsia and variable-interval bar-press performance. paper read at Psychon. Scie. meeting. Chicago, 1967.
(cited in Hawkins et al, 1972).

HAWKINS, T.D., SCHROT, J.F., GITHENS, S.H., and EVERETT, P.N. (1972) Schedule-induced polydipsia: an analysis of water and alchol ingestion. In: Gilbert, R.M., and Keehn, J.D. (eds). Schedule-effects: drugs, drinking and aggression. Toronto: Univ. Toronto Press.

HEBB, D.O. (1955) Drives and the C.N.S. (conceptual nervous system). Psychol. Rev., 62, 243-254.

HINDE, R.A. (1959) Unitary drives. Anim. Behav.,7, 130-141.

HINDE, R.A. (1960b) Energy models of motivation In: Beament, J.W.L. (ed). S.E.B. Symp. XIV., Models and analogues in biology. 199-213.

HINDE, R.A. (1966) Animal behaviour: A synthesis of ethology and comparative psychology (1st ed). N.Y: McGraw-Hill.

HINDE, R.R. (1970) Animal behaviour: A synthesis of ethology and comparative psychology. (2nd ed). N.Y: McGraw-Hill.

HINDE, R.A., and STEVENSON-HINDE, J. (1973) Constraints on learning: limitations and predispositions. London, N.Y: Academic Press.

HODOS, W., and CAMPBELL, C.G.B. (1969) Scala naturae: Why there is no theory in comparative psychology. Psychol. Rev., 76, 337-350.

HOLST, E. von, and MITTELSTAEDT, H. (1950) Das Reafferanzprinzip. Naturwiss., 37, 464-476.

HOLST, E. von., and MITTELSTAEDT, H. (1954) Relation between the C.N.S. and the peripheral organs. Brit. J. Anim. Behav., 2, 89.

IERSEL, J.J.A. van., and BOL A.C.A. (1958) Preening of two tern species. A study on displacement activities. Behav., 13, 1-88.

KEEHN, J.D. (1970) Schedule-induced licking and polydipsia. Psychol. Rep., 26, 155-161.

KEEHN, J.D., and COLOTLA, V.A. (1971) Schedule-induced drinking as a function of interpellet interval. Psychon. Scie., 23, 69-71.

KILLEEN, P. (1975) On the temporal control of behaviour. Psych. Rev., 82, 89-115.

KING, G.D., and SCHAEFFER, R.W. (1973) Developmental analysis of schedule-induced polydipsia. Psychol. Rep., 32, 1087-1095.

KIRKMAN, F.B. (1937) Bird behaviour London: Nelson.

KORTLANDT, A. (1940) Wechselwirkung Zwischen Instinkten. Arch. Neerl. Zool., 4, 404-442.

KUO, Z.Y. (1967) The dyhamics of behaviour development: an epigenetic view. N.Y: Random House.

KUTSCHER, C.L. (1969) Species differences in the interaction of feeding and drinking. Annals N.Y. Acad. Scie., 157, 539-552.

KUTSCHER, C.L., STILLMAN, R.D., and WEISS, I.P. (1968a) Food deprivation polydipsia in gerbils Physiol and Behav., 3, 667-671.

KUTSCHER, C.L., STILLMAN, R. D., and WEISS, I.P. (1968b) Food deprivation polydipsia in hamsters. Psychon Scie., 11, 243-244.

LEHRMAN, D.S. (1953) A critique of Konrad Lorenz's theory of instinctive behaviour. Quart. Rev. Biol., 28, 337-363.

LEHRMAN, D.S. (1970) Semantic and conceptual issues in the nature - nurture problem. In: Aronson, L.R. et al (eds). Development and evolution of behaviour: essays in memory of T.C. Schneirla. San Francisco: Freeman and Coy.

LESTER, D. (1961) Self-maintenance of intoxication in the rat. Quart. J. Stud. Alcoh, 22, 223-231.

LEVITSKY, D.A. (1967) Psychogenic wheel running. Psychon Bull., 1, 35.

LEVITSKY, D.A., and COLLIER, G. (1968) Schedule-induced wheel running. Physiol. & Behav., 3, 571-573.

LEYHAUSEN, P. (1956) Verhaltensstudien bei Katzen. Z. Tierpsychol., Sppl. 2.
(cited in Delius, 1967).

LOCKHARD, R.B. (1968) The albino rat: a defensible choice or a bad habit. Amer. Psychol., 23, 734-742.

LOCKHARD, R.B. (1971) Reflections on the fall of Comparative Psychology. Amer. Psychol., 26, 168-179.

LORENZ, K.Z. (1937) Uber die bildung Instinktbegriffes in: Schiller, C. (ed). Instinctive behaviour. N.Y: International Univ. Press (1957).

LORENZ, K.Z. (1950) The comparative method of studying innate behaviour patterns. Symp. Soc. Exp. Biol., 4, 221-268.

LORENZ, K.Z. (1954) Psychologie und Stammesgeschte in: Heberer, G. (ed) Die Evolution der Organismen. Jena: Fischer.

LOTTER, E.C., WOODS, S,C., and VASSELLI, J.R (1973) Schedule-induced polydipsia: an artifact. J. Comp. Physiol. Psychol., 83, 478-484.

LUBAR, J.F., HERRMAN, T.F., MOORE, D.R., and SHOUSE, M.N. (1973) Effects of septal and frontal ablations on species-typical behaviour in the cat. J. Comp. Physiol. Psychol., 83, 260-270.

MacARTHUR, R.H. (1972) Geographical ecology: patterns in the distribution of species. N.Y: Harper & Row. (cited Falk, 1977).

MARSHALL, W.H. (1963) The ecology of mustelids in New Zealand. N.Z.D.S.I.R. publication, Information series No 38.

McDOUGALL, W. (1932) The energies of man. London: Methuen.

McFARLAND, D.J. (1966) On the causal and functional significance of displacement activities. Z. Tierpsychol., 23, 217-235.

McFARLAND,D.J. (1970b) Adjunctive behaviour in feeding and drinking situations. Rev. Comp. Animal, 4, 64-73.

McFARLAND, D.J. (1971) Feedback mechanisms in animal behaviour. London: Academic Press.

McFARLAND, D.J. (ed) (1974) Motivational control systems analysis London: Academic Press.

McNab, B.K. (1963) Bioenergetics and the determination of home range size. Amer. Naturalist., 97, 113-140 (cited Falk, 1977).

MELLO, N.K. (1968) Some aspects of the behavioural pharamacology of alchol. In: Efron, D.H. et al (eds), Pharamacology: a review of progress. Washington, D.C: U.S. Govt. Printing Office.

MENDELSON, J., and CHILLAG, D. (1970) Schedule-induced air licking in rats. Physiol. and Behaviour 5, 535-537.

MENDELSON, J., and CHILLAG, D. (1970) Tongue cooling: a new reward for thirsty rodents. Scie., 170, 1418-1421.

MOORE, B.R. (1972) The role of directed Pavlovian reactions in simple instrumental learning in the pigeon. In: Hinde, R.A. and Stevenson-Hinde, J.S.(eds) Constraints on learning. 1973. Academic Press: London, N.Y.

PALFAI, T., KUTSCHER, C.L., and SYMONS, J.P. (1971) Schedule-induced polydipsia in the mouse. Physiol and Behav., 6, 461-462.

PARMEGGIANI, P.L. (1962) Title unknown. Helv. Physiol. Pharmacol. Acta., 20, 347. (cited in Delius, 1967).

PAVLOV, I.P. (1927) Conditioned reflexes. London: Oxford Univ. Press.

PAVLOV, I.P. (1928) Lectures on conditioned reflexes. N.Y: International Publishers.

POLLARD, J.S., and LEWIS, R.F.U. (1968) Ferrets do learn mazes. J. Biol. Psychol., 11, 40-43.

PORTER, J.H., and KENSHALO, D.R. (1974) Schedule-induced drinking following omission of reinforcement of the rhesus monkey. Physiol. and Behav., 12, 1075-1077.

PORTER, J.H., SOZER, N.N., and MOESCHL, T.P. (1977) Schedule-induced polydipsia in the guinea pig. Physiol. and Behav., 19, 573-575.

REYNIERSE, J.H. (1966) Excessive drinking in rats as a function of number of meals. Canad. J. Psychol., 20, 82-86.

ROLL, D., SCHAEFFER, R.W., and SMITH, J.C. (1969) Effects of conditioned taste aversion on schedule-induced polydipsia. Psychon. Scie. 16, 39-41.

ROWELL, C.H.F., (1961) Displacement grooming in the chaffinch. Anim. Behav., 9, 38-63.

SCHAEFFER, R.W., DIEHL, J.C., and SALZBERG, C.L. (1966) An application of Premack's theory to behaviours associated with a F.F.I. food schedule. Psychon. Sci., 6, 405-406.

SCHAEFFER, R.W., and SALZBERG, C.L. (1967) Schedule-induced polydipsia: an atypical case. Psychol. Rep., 20, 1071-1076.

SCHAEFFER, R.W., and SALZBERG, C.L. (1973) Licking response distributions associated with the aquisition of schedule-induced polydipsia. Bull Psychon. Soc., 2, 205-207.

SCHUSTER, C.R., and WOODS, J.H. (1966) Schedule-induced polydipsia in the rhesus monkey. Psychol. Rep., 19, 823-828.

SEGAL, E.F. (1965) The development of water drinking on a dry-food free-reinforcement schedule. Psychon. Scie., 2, 29-30.

SEGAL, E.F. (1969a) The interaction of psychogenic polydipsia with wheel running in rats. Psychon. Sci., 14, 141-144.

SEGAL, E.F. (1969b) Transformation of polydipsic drinking into operant drinking: A paradigm? Psychon. Scie., 16, 133-135.

SEGAL, E.F. (1972) Induction and the provenance of operants. In: Gilbert, R.M., and Millenson, J.R. (eds) Reinforcement: behavioural analysis. N.Y: Academic Press.

SEGAL, E.F., and DEADWYLER, S.A. (1965) Water drinking patterns under several dry food reinforcement schedules. Psychon Scie., 1, 271-272.

SEGAL, E.F., and HOLLOWAY, S.M. (1963) Timing behaviour in rats with water drinking as a mediator. Scie., 140, 888-889.

SEGAL, E.F., and ODEN, D.L. (1965) Determinants of polydipsia in rats: a reply to Stein. 1. Emptying the water bottle. Psychon. Scie., 1, 201-202.

SEGAL, E.F., and ODEN, D.L. (1969) Schedule-induced polydipsia: effects of providing an alternative reinforced response and of introducing a lick-contingent delay in food delivery. Psychon. Scie., 15, 153-154.

SEGAL, E.F., ODEN, D.L., and DEADWYLER, S.A. (1965) Determinants of polydipsia: IV. Free-reinforcement schedules. Psychon. Scie., 3, 11-12.

SELIGMAN, M.E.P. (1970) On the generality of the laws of learning. Psychol. Rev., 77, 406-418.

SELIGMAN, M.E.P., and HAGER, J.L. (1972) Biological boundaries of learning. N.Y: Appleton-Century Crafts.

SEVENSTER, P. (1961) A causal analysis of a displacement activity (Fanning in Gasteroteus aculeatus. L.) Behav. Supplem., 9, 1-170.

SHANAB, M.E., and PETERSON, J.L. (1969) Polydipsia in the pigeon. Psychon. Scie., 15, 51-52.

SIDMAN, M. (1960) Normal sources of pathological behaviour. Scie., 132, 61-68.

SKINNER, B.F. (1938) The behaviour of organisms. N.Y: Appleton-Century-Crofts.

SKINNER, B.F. (1948) "Superstition" in the pigeon. J. Exp. Psychol., 38, 168-172.

SKINNER, B.F. (1956) A case history in scientific method. Amer. Psychol., 11, 221-233.

SKINNER, B.F. (1959) A case history in scientific method. In: KOCH, S. (ed) Psychology - a study of a science. N.Y: McGraw-Hill. vol 2.

SLANGEN, J.L., and WEIJNEN, J.A.W.M. (1972) The reinforcing effect of eletrical stimulation of the tongue in thirsty rats. Physiol. and Behav., 8 565-568.

STADDON, J.E.R., and SIMMELHAG, V.L. (1971) The superstition experiment: a reexamination of its implications for the principles of adaptive behaviour. Psych. Rev., 78, 3-43.

STEIN, L. (1964) Excessive drinking in the rat: superstition or thirst? J. Comp. Physiol. Psychol., 58, 237-242.

STRICKER, E.M., and ADAIR, E.R. (1966) Body fluid balance, taste, and postprandial factors in schedule-induced polydipsia. J. Comp. Physiol. Psychol., 62, 449-454.

STROMINGER, J.L. (1946) The relation between water intake and food intake in normal rats and in rats with hypothalmic hyperphagia. Yale. J. Biol. Med., 19, 279-288.

SYMONS, J.P., and SPROTT, R.C. (1976) Genetic analysis of schedule-induced polydipsia. Physiol. and Behav., 17, 837-839.

TEITELBAUM, P. (1966) The use of operant methods in the assessment and control of motivational states. In: Honig, W.K. (ed) Operant behaviour: areas of research and application. N.Y: Appleton-Century Crofts.

TINBERGEN, N. (1940) Die Uebersprungbewegung. Z. Tierpsychol., 4, 1-40.

TINBERGEN, N. (1951) The study of instinct. Oxford: Clarendon Press.

TINBERGEN, N. (1952) "Derived" activities, their causation, biological significance and emancipation during evolution. Quart. Rev. Biol., 27, 1-32.

TOATES, F.M. (1971) The effect of pretraining on schedule-induced polydipsia. Psychon. Scie., 23, 219-220.

TOLMAN, E.C. (1926) The nature of fundamental drives. J. Abnorm Soc. Psychol., 5, 349-358.

ULRICH, R.E., and AZRIN, N.H. (1962) Reflexive fighting in response to aversion stimulation. J. Exp. Anal. Behav., 5, 511-520.

VALENSTEIN, E.S., COX , V.C., and KAKOLEWSKI, J.W. (1969) The hypothalamus and motivated behaviour. In: Tapp, J.T. (ed) Reinforcement and behaviour. N.Y: Academic Press. 242-283.

VALENSTEIN, E.S., COX, V.C., and KAKOLEWSKI, J.W. (1970) Reexamination of the role of the hypothalamus in motivation. Psychol. Rev., 77, 16-31.

VERPLANK, W.S., and HAYES, J.R. (1953) Eating and drinking as a function of maintenance schedule. J.Comp. Physiol. Psych., 46, 327-333.

VILLAREAL, J.E. (1967) Schedule-induced pica. Paper read at meeting of Eastern Psychological Association, Boston. April, 1967. (cited in Falk, 1969).

WARDEN, C.J. (1931) Animal motivation: experimental studies on the albino rat. N.Y: Columbia Univ. Press.

WAYNER, M.J. (1970) Motor control functions of the Lateral Hypothalamus and adjunctive behaviour. Physiol. and Behaviour., 5, 1319-1325.

WAYNER, M.J. (1974) Specificity of behavioural regulation. Physiol. and Behav., 12, 851-869.

WAYNER, M.J., GREENBERG, I., TATAGLIONE, R., NOLLEY,D., FRALEY,S., and COTT. (1972) A new factor affecting the consumption of ethyl alcohol and other sapid liquids. Physiol. and Behav., 8, 345-362.

WAYNER, M.J., and GREENBERG, I. (1973) Schedule dependence of schedule-induced polydipsia and lever pressing. Physiol. and Behav., 10, 965-966.

WAYNER, M.J., GREENBERG, I., FRALEY, S., and FISHER,S. (1973) Effects of Δ^9 - tetrahydrocannabinol and ethyl alcohol an adjunctive behaviour and the lateral hypothalamus. Physiol. and Behav., 10, 109-132.

WEIJNEN, J.A.W.M. (1972) Lick-contingent electrical stimulation of the tongue: its reinforcing properties in rats under dipsogenic conditions. Ph. D. thesis. Univ. Utrecht. private publication. Utrecht: Elinkwijk.

WHALEN, T.E., and WILKIE, D.M. (1977) Failure to find schedule-induced polydipsia in the pigeon. Bull. Psychon. Soc., 10, 200-202.

WHITE, S.D., WAYNER, M.J., and COTT, A. (1970) Effects of intensity, water deprivation, prior water ingestion and palatibility on drinking evoked by lateral hypothalamic electrical stimulation. Physiol. and Behav., 5, 611-619.

WILLIAMS, D.R., and WILLIAMS, H. (1969) Auto-maintenance in the pigeon: sustained pecking despite contingent non-reinforcement. J. Exp. Anal. Behav., 12, 511-520.

WILSON, S., and SPENCER, W.B. (1975) Schedule-induced polydipsia: species limitations. Psychol. Rep., 36, 863-866.

WOODS, P.J. (1962) Behaviour in a novel situation as influenced by the immediate preceeding environment. J. Exp. Anal. Behav., 5, 185-190.

ZEIGLER, H.P. (1964) Displacement activity and motivational theory: a case study in the history of ethology. Psychol. Bull., 61, 362-376.

A P P E N D I X O N E

ANIMAL BEHAVIOUR: SOME CURRENT ISSUES AND PROBLEMS.

(A) An Historical Perspective.

(B) Comparative Psychology.

- (1) Introduction and origins.
- (2) Contemporary problems.
  - (i) "Subject and behaviour-process myopia".
  - (ii) The species studied: phylogenetic relatedness.
  - (iii) Semantic imprecision.
- (3) An overview.

(C) Behaviourism.

- (1) Origins.
- (2) The search for an all-encompassing theory.
- (3) Skinner and the operant analysis of behaviour.
- (4) A changing emphasis.

(D) Ethology.

- (1) Origins and emphases.
- (2) The era of controversies.
- (3) Contemporary features of ethology.

(E) In Summary.

(F) References.

A N I M A L B E H A V I O U R: S O M E

C U R R E N T I S S U E S A N D P R O B L E M S.

As has been discussed in the Introduction, a re-appraisal of Animal Behaviour has been evident in the 1970's and contrasts with the earlier polarization of the different theoretical approaches to the subject. These differing disciplines embrace a number of methodological and philosophical approaches that have often been irreconcilable, and have often generated acrimonious debate that has tended to obscure rather than elucidate. This essay considers selected aspects of the study of animal behaviour, with a particular emphasis upon the issues facing comparative psychology. This emphasis does not imply a pre-eminence of comparative psychology over other approaches to animal behaviour; rather it indicates a personal view that this particular approach reflects the greatest reappraisal of the theoretical and methodological issues in contemporary thinking on the behaviour of animals.

(A) An Historical Perspective.

Historically, observations of animal behaviour predate writing, as pre-historic drawing indicates an interest in the subject apparently from viewpoints of

survival and worship. (See Warden, 1927, for a consideration of these early Historical aspects of animal behaviour). However, religious considerations pervaded evaluation of the topic until the time of Darwin, for until this point the systematic study of animal behaviour was related to theological necessity. Debates as to the likely possession of a soul may have been beneficial to theology, but served little value to understanding why animals behave as they do. Despite the disinterest in the behaviour of animals *per se*, important concepts emerged from this period, and many of these set intellectual precedents in the contemporary thinking on the subject. Most notably, these include;

(i) Aristotle's *Scala naturae* (the precursor of the contemporary phylogenetic scale).

(ii) Instinct and intelligence (attributed to the medieval scholastics circa 1400 A.D.).

(iii) Descartes' formulations on the mind/body problem (the mechanistic philosophy often reflected in Behaviourism).

(iv) Lamarck's theory of evolution (in which behaviour was systematically embodied as a subject into a biological theory).

However, it was the contribution of Charles Darwin that provided the most significant impact upon the early study of animal behaviour.

Darwins' theory of evolution instigated an unparalleled reappraisal of scientific, theological and philosophical issues, producing a major transformation of the existing body of knowledge. Animal behaviour was seen

to be a legitimate topic in its own right, devoid of theological considerations, and important as an agent of evolutionary change. This was particularly emphasised in *"The Descent of Man"* (1871), and *"The Expression of the Emotions in Man and the Animals"*, (1872).

> "Darwins' own main contribution, the theory of selection, also involved essential relationships between behaviour and evolution. He saw and illustrated with many examples that the behaviour of animals is often determined, and always circumscribed, by their heredity, although he knew even less than we do about the mechanisms involved. The behaviour of animals is also obviously and crucially involved in their survival and success in reproduction. Thus natural selection provides another way, less direct, but truer than the supposed Lamarkian way, in which behaviour is bound in with the changes in heredity that constitutes evolution". (Simpson, 1958, P.8).

The study of intelligence was among the first topics to benefit from this theoretical approach, efforts being directed towards the discovery of signs of incipient mentality in animals, that would be expected if the mind of man was on the same continuum as them. Also, the study of instinct featured prominently. These two topics were of fundamental importance to the later subjects of

comparative psychology and ethology.

The post-Darwinian era was characterised by a flourishing interest in animal behaviour from a theoretical and research viewpoint, in which the prime consideration was based upon further elucidation of evolutionary processes through the study of behaviour. And along with this expansion in interest in animal behaviour came contentious debate over various issues; in particular the use of anthropomorphism and the anecdotal method. Stemming from the writings of G.J. Romanes, a large number of papers appeared in which the existence of "higher" behaviours in animals was discussed, often on a level of incredulity rivalling the statements of the Roman author Pliny, (who would have "dogs howling at the moon in worship", and "elephants ritually bathing at evening to purify body and spirit".) To the biologists studying animal behaviour, such conclusions ran contrary to their training in scientific objectivity, and the use of anthropomorphism and anecdotalism were rejected as being unreliable, subjective, and scientifically disreputable. However, a deeper issue was implicit in this dispute - the basic philosophical discontinuity between mechanism and vitalism. The promulgation of the "law of parsimony" (Lloyd Morgan, 1894) had great impact upon consequent approaches to animal behaviour, and provided a cornerstone to this science (with its most extreme expression being found in the contemporary philosophy of radical behaviourism).

The differences between mechanistic and vitalistic philosophies had significance beyond the rejection of

anecdotal methods, for this issue focussed upon the differences between the biologists (who were seeking further exploration of the evolution of instinct and intelligence) and the early psychologists (who were primarily of philosophical outlook). Of this period, Scott (1973) notes:

> "In this era work was at first dominated by biologists; before 1890 there were few individuals who called themselves psychologists, and even these were still creeping out of that mother fold of sciences, philosophy. The collection of data was dominated by two concepts, the evolution of intelligence, and the evolution of instinct, which were seen as forming a distinct dichotomy.

However, the interest in behaviour by the biologists was soon to diminish, as Mendel's research on genetics was re-discovered at the turn of the century and led to the theories of chromosomal transmission of heredity and of the gene within a few years.

> "Most of the biologists (including T.H. Morgan himself) switched their attention away from animal behaviour and devoted it to the new science of genetics, which was so promising of fruitful results".
> (Scott, 1973)

About this time another significant change in emphasis occurred, one which strongly influenced the

development of animal psychology. Pavlov's research on conditional reflexes focussed interest upon the process of learning, and away from considerations of the evolution of intelligence. Hence the psychological tradition of learning research became established, along with the use of standard laboratory animals to study learning processes, and the advent of "rat psychology".

> "Since most psychologists of that day were poorly supported, they used the cheapest available mammal, which happened to be the Norway rat, rather than the dog". (Scott, 1973).

A concurrent development was the setting up of research laboratories and teaching courses in animal psychology, most notably in the U.S.A., where this learning-oriented tradition has remained steadfast since.

No specific time or event can be defined when the contemporary approaches to animal behaviour became specifically identified; rather, a gradual coalescence of methodologies and philosophical adherences came about, leading to the various "schools" of study. Generally, these schools can be identified under the headings of Comparative Psychology, Behaviourism, and Ethology.

(B) COMPARATIVE PSYCHOLOGY.

(1) Introduction and Origins.

The term comparative psychology was first used by

Flourens in 1864 as the title of a book. Jaynes (1969) views this book as the starting point of the subject:

> "It was partly a rewrite of an earlier work (Flourens 1861), but he added among other things a new first chapter and probably, to counteract the non-Cuvier connotations of ethology founded 6 years earlier, re-titled the book *Psychologie Comparée*. While it is possible that the term may have been used earlier in a trivial way, this is the first attempt to found comparative psychology as a new science. In the first chapter, Flourens is quite conscious of this. Comparative psychology is to combine human psychology as it is represented in Descartes, i.e. from a mechanistic neurological stand-point, and animal psychology as it has been represented by Reamus, Leroy and Cuvier".

In the decade 1875-1885 there were no fewer than five books published with comparative psychology as their title; Joly (1877), Vignoli (1877), Espinas (1877), Tissot (1878), and Bascom (1878); and the term was also used as the title of an article by Herbert Spencer in 1875, while Romanes had made clear reference to it in two of his books published in 1883 and 1884. It is difficult to define the beginning of comparative psychology; rather its development was one of a coalescence of a number of theoretical concepts, and the first products of experiment-

tation, as is suggested by Jaynes,

> "It is impossible to know when a new name for something is needed. But how quickly it is taken up, if at all, is certainly an indication of that need. And immediately the phrase, comparative psychology, was spoken of everywhere".

Although Romanes was the first major name associated with the term (following the Darwinian ambition to demonstrate the continuity of mental traits over the phylogenetic scale) his work was criticised on the grounds of subjectivity, and the emphasis became centred upon experimental and laboratory-based research principles. Lubbock is generally credited with being the first person to employ laboratory techniques in his research, and he led the way for an approach focussing upon what animals were capable of doing under a set of rigidly controlled laboratory principles. With a shifting emphasis away from naturalistic settings towards the experimental laboratory came the rise into pre-eminence of the American schools of Comparative Psychology to a position they have occupied ever since. Naturalistic approaches to animal behaviour did however, remain popular in Europe, although these two divergent viewpoints did not come into mutual contact until the 1950's.

In 1898 E.L. Thorndike, a distinguished comparative psychologist, commenced publication of his work, while concommitantly, Kline started the first laboratory course in this subject. In the following year another

distinguished comparative psychologist, R.M. Yerkes, established his laboratory at Harvard University, and in 1903 the founder of Behaviourism, J.B. Watson followed suit at Chicago University. (for further consideration of these early researchers see Tobach, Adler and Adler, 1973).

The history of comparative psychology has characteristically been fraught with issues and disagreements. In general, these disputes reduce to a few issues that may be summarised as relating to what subject areas are subsumed under the term "comparative psychology", as to whether inter-species differences are a main concern of this approach, and as to what methodological manipulations constitute valid tools of research. Numerous writings over the last sixty years have proffered divergent opinions as to what Comparative Psychology was really concerned about, and this question is still unanswered. The contemporary student of this discipline may justifiably claim doubt as to whether it really exists, as is exemplified by the titles of the following papers, all published in the early 1970's: *Reflections on the fall of Comparative Psychology* (Lockhard, 1971)., *Comparative Psychology is not dead* (Adler & Tobach 1971)., *On the demise of Comparative Psychology* (Harless, 1971)., *On the fall of Comparative Psychology* (Boice 1971).,*Comparative Psychology lives on under an assumed name - Psychogenetics* (Wilcox, 1972).

Beyond the emotive claims and counterclaims of such articles there remains a substantial body of research and theory about comparative psychology that has been accrued over this century.

For a comprehensive review of research and historical developments in Comparative Psychology reference should be made to the following texts: *Introduction to Comparative Psychology* (Morgan, 1904)., *Animal Intelligence* (Romanes, 1910)., *Animal Intelligence* (Thorndike, 1911)., *Behaviour: An Introduction to Comparative Psychology* (Watson, 1914)., *Outline of Psychology* (McDougall, 1923)., *Purposive Behaviour in Animals and Men* (Tolman, 1932)., *Comparative Psychology: A Comprehensive Treatise* (Warden, Jenkins & Warner, 1935)., *Principles of Animal Psychology* (Maier and Schneirla, 1935)., *The Animal Mind* (Washburn 1936)., *Animals and Men: Studies in Comparative Psychology* (Katz, 1937)., *Comparative Psychology* (Moss, 1942)., *Comparative Psychology* (Stone, 1951)., *Learning and Instinct in Animals* (Thorpe, 1956)., *Animal Behaviour* (Scott, 1958)., *Principles of Comparative Psychology* (Waters Rethlingshafer and Caldwell,1960)., *Comparative Psychology* (Ratner and Denny, 1964)., *Animal Behaviour* (Breland and Breland, 1966)., *Animal Behaviour* (Breland and Breland, 1966)., *Animal Behaviour* (Hinde, 1966)., *Comparative Psychology at Issue* (Tobach, Adler, and Adler, 1973).

(2) Contemporary Problems.

Unlike the abovementioned texts, which generally contain information on a more mundane and prosaic level, a number of recent articles have appeared that criticise comparative psychology on a number of issues. These issues are often seen as being interrelated, but generally can be separated into three problems areas, namely,

(i) an overdependance on the white rat and

learning process studies,

(ii) the theoretical basis for making phylogenetic comparisons and the assumptions of a "phylogenetic scale",

(iii) and, the semantic confusions relating to the use of the word "comparative".

These problem areas will be considered separately.

(i) "Subject and behaviour-process myopia."

In his classic paper "The Snark was a Boojum" Beach (1950) introduced a debate about the overdependance on the white-rat and learning process experiments in comparative psychology. His strictures as to the inadvisability of relying upon the laboratory rat as an experimental subject have remained to the greater extent, accepted, as papers in the *American Psychologist* indicate (e.g. Dukes, 1960; Whalen, 1961; Bitterman, 1965; Yeager, 1973). These papers have analysed the type of experimental animals used, and the type of behaviour studied, over successive publications of the *Journal of Comparative and Physiological Psychology*. They confirm that there is a preponderance of learning and conditioning studies based upon the rat, and these conclusions have been used to "reaffirm Beach's message of subject and behaviour-process myopia" (Yeager, 1973). The consequences of this limited approach to the study of animals and their behaviour appear to have been serious for comparative psychology, alleges one author.

"According to Lockhard (1971) it was the questioning of these and related dogmatic traditions which inevitably

> resulted in the replacement of comparative psychology with a new evolutionary-concious field, animal behaviour". (Yeager, 1973).

The veracity of many of the points raised in these papers notwithstanding, some questioning of the methods used to quantify trends in comparative psychological research seems necessary on a number of grounds. Firstly, most of these papers investigating the "trend of contents" of the *Journal of Comparative and Physiological Psychology* appear to ignore other publications that contain animal-related research, such as: *Behaviour, Psychonomic Science, The Psychological Record, Physiology & Behaviour, The Journal of Genetic Psychology* and *Animal Behaviour*. As Yeager states,

> "an implicit assumption has been made, namely that the scope of American comparative psychology is exemplified by articles published in JCPP".

He presents evidence which shows a "paucity of concern with the rat conditioning and learning" in a similar analysis conducted on *Behaviour*. Secondly, the use of the adjective "comparative" in the title of the *Journal of Comparative and Physiological Psychology* seems inappropriate, as this journal publishes few articles of a comparative psychological nature, such that its' editorial policy must be questioned:

> "Rather than comparative psychology *in toto* being criticized for an unwarranted emphasis on the rat and

> on learning, the editorial policy of a journal professing to publish work of a comparative nature may be criticized,..... with this in mind, perhaps the editors of JCPP would do well to delete the work "comparative" from the title of that journal and thus attain a more meaningful description of its contents".
> (Yeager)

Essentially this statement is a reaffirmation of Lorenz's (1950) views on this journal:

> "I must confess that I strongly resent it, not only from the terminological viewpoint, but also in the interests of the very hard-working and honest investigators, when an American journal masquerades under the title of "comparative" psychology, although to the best of my knowledge, no really comparative paper has been published in it".

Thus some questioning of methods used to assess the "limited scope of comparative psychology" seems necessary; but these questions aside, it would appear that there are valid criticisms of this approach, that are perhaps best summarised by Schneirla (1966) who, in speaking of the range of species published in the *Journal of Comparative and Physiological Psychology*, was moved to note

that,

> "devotion is strong to specialised problems along restricted lines, but is weak to problems of comparative significance".

(ii) The species studied: phlyogenetic relatedness.

Beyond Beach's criticism that an over-reliance upon the rat promotes a limited outlook in comparative psychology, have been other papers that have challenged the use of this species on the grounds of; the peculiar genetic basis of selection in this animal (Lockhard, 1968; for an expanded discussion of this issue see Appendix Two); that parallels drawn from rats to other species promote "capricious comparisons" (e.g. Ratner and Denny, 1964; Hodos and Campbell, 1969; Lockhard, 1971); and that the traditional concept of a phylogenetic scale along which animals may be arranged is at variance with modern views on evolution (Hodos and Campbell, 1969). This latter point provides an important challenge to the reasons for selecting various species for study, as Hodos and Campbell (1969) state:

> "However, much of the current research in comparative psychology seems to be based on comparisons between animals, that have been selected for study *according to rather arbitrary considerations and appears to be without any goal other than the comparison of animals for the sake of comparison*".
> (Italics mine).

They demonstrated that the Aristotelian ambition to order all species along a dimension of increasing complexity has long been implicit in the theory of comparative Psychology, that this view does not concur with modern biological knowledge on evolution, and that,

> "The widespread failure of comparative psychologists to take into account the zoological model of animal evolution when selecting animals for study and when interpreting behavioural similarities and differences has greatly hampered the development of generalizations with any predictive value".

Hodos and Campbell strongly criticise the apparent confusion of comparative psychologists in failing "to distinguish between data obtained from living representatives of a common evolutionary lineage and data from animals which represent divergent lineages", and they recommend a series of alternatives to correct this problem. These include a description of the behavioural capacities of organisms throughout the animal kingdom, emphasis upon finding systematic trends in behaviour capable of varying reliably with other taxonomic indices, efforts to reconstruct the historical development of behaviour, and an analysis of the general mechanisms of adaptation and survival. Beyond providing these alternatives, they challenge practices that have, "had the effect of over-simplifying an extremely complex field of research". This is interpreted as a criticism of the

tendency to indulge in unwarranted and invalid generalisation.

Generalisation between species, or within species, presents a difficulty relating to what Ratner and Denny (1964) term "capricious comparisons", in that it is frequently invalid to apply generalisations to arbitrary groups of animals. This problem is discussed by Harlow, Gluck and Suomi (1972), in which they note:

> "Most biologically trained scientists are of the opinion that generalisation from nonhuman behavioural data to man is justifiable, and they differ only in the degree to which they believe this to be true. Some biological scientists are convinced that there are behavioural areas beyond the pale, whereas other scientists pale at any suggestion relative to interspecies generality. There is only one way to test the limits of interspecies generalization and that is by experimentation: ..... From the point of view of cold facts - and most facts are - it is commonly believed that some animal data generalise to man and some do not. The only problem then is that of selecting between or among the data that generalise and those who do not. This is never an easy task since there is no completely logical or objective way to make the separation".

While Harlow *et al* may be correct in that there are no simple rules governing interspecies generality, it would seem advisable to base any generalisations upon some clearly defined theoretical basis, and not engage in "capricious comparisons" as a perfunctory routine without regard to overall theory. Hodos and Campbell take exception to naive generalisations about phylogenetic relatedness, citing Bitterman (1965a, 1965b) as a culprit who applies labels such as "fishlike", "ratlike" to comparative data without regard to the evolutionary processes that have operated upon his various experimental species to produce similarities and differences in their respective behaviours.

In general, it would seem that comparative psychology has often ignored the findings of biology when generating theory and research practices, especially where a choice of species to compare is concerned. Also, generalisations from such data may have been naive and precipitat.

(iii) Semantic imprecision: the definition of comparative psychology.

Discussion of the usage of the adjective comparative in psychology is not solely a recent phenomenon, as is indicated by the following quotation:

> "It seems wholly desirable, therefore that we discard the present usage of comparative psychology and employ the term to designate the study of consciousness, behaviour, or the products of behaviour - no matter what the type of organism concerned - by the method of comparison..... This note on

> definitions is written with the hope that it may help to carry into oblivion the use of comparative psychology as synonymous with "animal psychology", and bring about the substituion of the natural, logical usage which the terms comparative and psychology, when linked, suggest".
> (Yerkes, 1913).

Since this statement was made, questions as to what the comparative approach entails have continued, and numerous definitions and methodological polemics have been issued. Compare the terse and strict definition of Lorenz (1950), with the generalized view of Gottlieb (1976).

> "Since the days of Charles Darwin the term "comparative" has assumed a very definite meaning. It indicates a certain rather complicated method of procedure which, by studying the similarities and disimilarities of homologous characters of allied forms, simultaneously obtains indications as to the phyletic relationships of these forms of life and as to the historical origin of the homologous characters in question".
> (Lorenz, 1950, cited in Gottlieb, 1976).
> "A liberal and workable definition of comparative psychology is desirable.

> To be meaningful, such a definition must involve evolutionary considerations in the sense of lineages, selection pressures, problems of conveyance and divergence, the adaptive character of species - typical behaviour, and the like". (Gottlieb, 1976).

A review of the literature reveals two key issues in this debate (a) what is the comparative method (?), and (b) whether a distinction should be made from animal behaviour (?). Inevitable, these questions are inter-related to some degree, although specific points are raised by each.

(a) What is the comparative method?: Relating to Yerke's definition, in which "the method of comparison" was emphasised, is the criticism that semantically this adjective can only apply to studies in which comparisons are made between two distinct groups. As Hodos and Campbell (1969) have noted of Beach's (1950) suggestion,

> "the term comparative psychology should be reserved for experiments in which organisms of different species are *compared*,"

and they have suggested that a specific emphasis of this approach would be,

> "on the similarities and differences between various taxonomic groups of organisms".

This view paraphrases a frequently cited description by Schneirla (1966), who again emphasizes "similarities and differences", but who introduces a wider extension of this

method beyond "animals on all phyletic levels" to include "individual abilities and behavioural intergration within groups". This method has been summarised into three basic points by Russell (1973), namely,

> "There are at least three basis for definition: first, that comparative psychology is a *body of knowledge* about behaviour in a variety of species of animals; second, that comparative psychology is a *methodological approach* to the study of behaviour; and third, that comparative psychology may be defined as employing *one of the logics of scientific method*".

This statement seems to embody important elements in the subject, without overly emphasising any one, and permits a comparative analysis between any suitable groups since this satisfies both methodological and theoretical requirements. Furthermore it permits fulfilment of one of the basic functions of the comparative method, the establishment of generalities, although as previously discussed, this depends upon a suitable theoretical justification.

(b) Distinctions from Animal Psychology: Debate continues as to whether the term comparative psychology should be reserved for experiments in which interspecies comparisons are made, and that other studies should be referred to as "animal psychology" (e.g. see Hodos and Campbell, 1969; Lockhard, 1971). This issue has generated divergent

opinions, such as that of Dewsbury (1973) who favours retention of the term comparative psychology on the grounds of tradition:

> "I am reluctant to discard a name that is associated with a great tradition, even though we may be in a period of great change. Tradition is one thing that is in a name".

In comparison, Ratner (1972) notes two issues, firstly that,

> "Comparative psychology is in need of redirection and reformulation. The second is that a distinction can be drawn between (a) an approach to comparative psychology typical of Zoologists and many animals behaviourists that emphasizes evolution and (b) an approach to comparative psychology that deals with behaviour of organisms and emphasizes the diversity of behaviour and its analysis by means of the comparative method".

Ratner emphasizes that the comparative method is seen,

> "as a sequence of stages of inquiry ranging from collecting background information about behaviours of organisms to postulating general

> mechanisms to explain diversity of behaviours".

and he further elaborates that the,

> "content of comparative psychology is drawn from studies of behaviours of organisms by animal behaviourists, general - experimental psychologists, and comparative psycholgists".

While he has admirably described the general features of this approach, it seems tautological to define the content of comparative psychology as being drawn from the work of comparative psychologists.

Zeigler (1973) delineates two rationales for the study of animal behaviour, both involving an evolutionary framework, but one of which does not concern itself to any extent with evolution, preferring to elucidate "general principles, general mechanisms, and general laws". The other rationale is integrally involved in evolutionary processes, in which "the similarities and differences among species constitute the very subject matter" of this approach, and in which "the comparative method is one of its prime research techniques".

In contrast to Ratner (1972), Zeigler sees evolutionary processes as the basic framework upon which the comparative method is applied, and thus distinctions between this, and general animal psychology are defined according to whether a general process is sought, and whether such generalized laws are anthropocentric in nature. This topic of anthropocentrism is a further issue in the debate as to what is comparative psychology, and what is simple animal

psychology.

In comparing these differing approaches Zeigler notes that the psychologist who tends towards anthropocentrism finds the behaviour of animals of interest,

> "only to the extent they exemplify a series of successive approximations to such human processes as learning, memory, emotion, aggression, and so on. He is therefore concerned primarily with similarities among species, and is relatively uninterested in differences between species that reflect adaptations to diverse environments".

Clearly such an approach cannot be considered comparative, because of the specific approach to the subject material, and because of a lack of interest in evolutionary processes *per se*. Yet studies are published purporting to be comparative psychology that do not meet this criterion. This is succinctly described by Thorpe (1973), who notes,

> "..... a great deal of what has been called by this name is not comparative psychology at all. The simple procedure of taking an animal, whether it be a cat, a rat, a fish, a snail, or an insect, and exposing it to a problem situation of a type that is primarily designed to test the responses of a human being does not necessarily and by itself

constitute an experiment in comparative psychology".

(3) An Overview.

In reviewing the issues raised, it is apparent that comparative psychology has always been subject to debate on its aims, methods and theoretical emphasis. However, many of these criticisms are couched emotively, and may be of less value as a consequence.

> "While the articles of self-criticism are good carthartics, comparative psychology should admit to the over-whelming influence of Watsonian environmentalism around us. Animals will perhaps always have limited value as models for human behaviour, but only as models, not animals". (Boice, 1971).
>
> "Could it be that Lockhard's extreme viewpoint makes him a bed-fellow of the Skinnerian who is similarily content with, nay insist-ent upon, explanation only at some particular and limited level? (Plotkin, 1971).
>
> "Perhaps the analysis of Lockhard and others should be received by comparative psychologists with delight rather than dismay. There has been some very radical

> rethinking in comparative
> psychology during the past decade.
> Psychologists working in other
> areas of the discipline may even
> come to regard it with envy".
> (Wilcox, 1972).

Such writings also reflect the changing emphasis and structure of comparative psychology, in which the lack of agreement as to the appropriate goals of this approach become apparent. Apart from referring to a specific scientific method (the method of comparison between two groups), the term "comparative psychology" has become synonymous with "animal psychology" (in which case the emphasis has been upon generalised learning abilities in a range of species without specific reference to evolutionary theory). Consequently, spurious and naive generalisations, upon a limited range of species and behaviour types have been common. Contemporary thinking on evolutionary theory has often been ignored, such that the Aristotelian concept of a phylogenetic *scala naturae* has remained a central concept in comparative psychology, although Biology had long rejected this as being naive, oversimplified, and anthropocentric.

The semantic useage of the words "comparative psychology" also reflects confusion, with divergent views being common. It is suggested that the term comparative psychology should be reserved for studies that use the comparative method, that such studies should relate to general biological approaches (e.g. evolution, genetics, ecology), that the study of animals is a legitimate subject

in its own right, and that those studies using animals in a noncomparative manner be subsumed under the general heading of animal behaviour. In attempting these goals, comparative psychology may achieve the goal originally proposed by Darwin, though long neglected in practice and theory. In general, the changing fabric of comparative psychology reflects the adoption of biological theory and the evolutionary perspective, with a consequent strengthening of the comparative approach. One may speculate that comparative psychology has at last been reunified with the philosophy of Biology and regained the vigour so evident in the early work on the evolution of behaviour, evident in the period 1875 - 1900.

(C) BEHAVIOURISM.

(1) Origins.

The term "behaviourism" was first used by Watson (1913, 1914), to describe a mechanistic approach to psychology which challenged the then current popularity of introspective and mentalistic methodologies. His choice of this term seems somewhat apologetic, as the footnote on the first page of his book *Behaviour: An Introduction to Comparative Psychology* (1914) would indicate,

> "A few new terms have been used in this discussion of behaviour - such as behaviourist, behaviouristic, behaviourism. While it is admitted that these words sound somewhat

> barbaric on a first hearing, they
> at least have the merit of being
> expressive and natural".

Although the relationship to cartesian mechanism is apparent in his writings, Watson indicated in this book his familiarity and association with Darwinian principles, as Herrnstein has noted in his introduction to the 1967 edition of this text. This view contradicts that of Kuo (1967), who implies that Watson was a non-Darwinian, and who ignores the considerable naturalistic research that Watson had conducted upon birds (see Gray, 1971). With respect to the study of animals, Watson clearly defined his Darwinian sympathies, as is evident in the first paragraph of his book, in which he states,

> "Psychology as the behaviourist
> views it is a purely objective
> experimental branch of natural
> science. Its theoretical goal
> is the prediction and control
> of behaviour ..... The
> behaviourist attempts to get a
> unitary scheme of animal response.
> He recognises no dividing line
> between man and brute.
> The behaviour of man, with all
> of its refinement and complexity,
> forms only a part of his total
> field of investigation".

Also this quotation indicates the mechanistic goal of "objectivity" and "prediction and control". The

basic issues in contemporary behaviourism are familiar, and reference to the rejection of instinctive behaviour (Kuo, 1921, 1924; Dunlap, 1919), the influence of Pavlovian reflexology (Pavlov, 1927), and an adherence to laboratory-based control (Skinner, 1938) require no further elucidation. Unlike comparative psychology, behaviourism started from a defined methodological (and theoretical [1]) viewpoint, such that its pre-eminence in the psychological studies on learning is understandable, especially in regard to the contributions of researchers such as Tolman, Hull and Skinner.

(2) The search for an all-encompassing theory.

The theoretical positions of Tolman and Hull reflect to some extent the differences between vitalistic and mentalistic approaches, for although both promoted a S-O-R formulation (with the O being defined as "intervening variables"), Tolman held that all behaviour, other than reflexive, was "purposive" i.e. goal-orientated. In contrast, Hull formulated a highly structural model in which the intervening variables modulated the input (S) and the output (R) in a quantifiable and empirically testable manner, since his model was derived from symbolic logic. Whereas Tomman saw his intervening variables as being not directly observable, Hull speculated and enumerated seventeen parameters that he had deduced from

1. Although Skinner disputes a theoretical adherence in his approach, it seems evident in his later writings that there is a considerable theoretical foundation to his thinking (e.g. Skinner, 1969).

his manipulations of logic. Both theorists purported to account for all behaviour, since both theories were aimed at elucidating the generalised laws governing the behaviour of higher organisms. e.g.

> "all behaviour of the individuals of a given species and that of all species of mammals, including man, occurs according to the same set of primary laws" (Hull, 1945 cited in Hinde, 1973).

In common, both theorists used laboratory based principles with the rat as a subject to achieve their formulations, and both used statistical and mathematical manipulations to give support to their conclusions. As Hinde (1973) has noted, their approach to behaviour typified that of the neobehaviourists of the thirties and fourties which was "characterised by a belief in the possibility of constructing a comprehensive theory of behaviour". In the search for generality, such theories were criticised as being simplistic and naive, (e.g. Lorenz, 1965; Seligman, 1970): and Hinde (1973) cites Tolman as remarking,

> "I think the days of such grandiose, all-covering systems is psychology as mine attempted to be are, at least for the present, pretty much passe' ".

Because their formulations were explicit, the theories of Hull and Tolman were quickly attacked, and found lacking, since their deductively-based predictions

were not supported by empirical evidence.

(3) Skinner and the operant analysis of behaviour.

The contribution of Skinner has been more enduring, largely because he eschewed explicit theory and the use of statistical manipulations, and because his views were inductively based upon the data his subjects produced. However, his position as a general process theorist has precluded consideration of species-typical behaviour in favour of elucidating generalised laws of learning. This is clear in his famous statement in 1959, in which he proclaimed:

> "Pigeon, rat, monkey, which is which? It doesn't matter. Of course, these species have behavioural repetoires which are as different as their anatomies. But once you have allowed for differences in the ways in which they make contact with the environment, and in the ways in which they act upon the environment, what remains of their behaviour shows astonishingly similar properties".

It is difficult to reconcile his acknowledgement of species-differences with the care he has taken to minimise such differences. While ignoring the importance of phylogenetic-factors he simultaneously refutes the possibility of these (denied) factors affecting his formulations. In this quotation he explicitly proclaims minimal interest in species-typical behaviour, yet in his 1969 book *Contingencies of Reinforcement* he states,

> "The ways in which animals behave compose a sort of taxonomy of behaviour comparable to other taxonomic parts of biology. Only a very small percentage of existing species has yet been investigated. (A taxonomy of behaviour may indeed be losing ground as new species are discovered). Moreover, only a small part of the repetoire of any species is ever studied. Nothing approaching a fair sampling of species-specific behaviour is therefore ever likely to be made".

This seems contradictory, since he has previously extoled the similarity of behavioural data obtained from different species, and then he decries the lack of inter-species research and denies the body of knowledge carefully compiled by such researchers as Schneirla, Lehrman, Tinbergen, Hinde, Lorenz etc. Further confusion is added when Skinner (1969) counters criticism as to the over-reliance upon pigeon and rat data, obtained from these highly domesticated species in the Skinner box:

> "Domesticated animals offer many advantages. They are more easily handled, they thrive and breed in captivity they are resistant to the infections encountered in association with man, and so on. Moreover, we are primarily interested

> in the most domesticated of all animals - man. Wild animals are, of course, different - possibly as different from domesticated varieties as some species are from others, but both kinds of differences may be treated in the same way in the study of basic processes".

Thus his view is homocentric, placing species differences on a level of unimportance, since such differences can be accounted for by understanding the basic processes alone. This view is merely a re-statement of the cartesian mechanism in a slightly more contemporary form. Beyond the philisophical quaintness of his view, his understanding of evolutionary and ecological processes seems naive, since he adamantly adheres to a belief in the suitability of the laboratory environment as the best way to study behaviour:

> "The behavioural taxonomist may also argue that the contrived environment of the laboratory is defective since it does not evoke characteristic phylogenic behaviour. A pigeon in a small enclosed space pecking a disk which operates a mechanical food dispenser is behaving very differently from pigeons at large. But in what sense is this behaviour not "natural"? If there is a natural phylogenic environment, it must be the environment in which a given kind of behaviour evolved.....

> Current environments are almost as "unnatural" as a laboratory. In any case, behaviour in a natural habitat would have no special claim to genuiness. What an organism does is a fact about that organism regardless of the conditions under which it does it. A behavioural process is none the less real for being exhibited in an arbitrary setting". (Skinner, 1969)

Such a viewpoint is questionable on several grounds; it seems to deny the adaptiveness of behaviour in the non-laboratory environment; it assumes that behavioural evolution occurred a long time ago and has now ceased to operate (ignoring the very plasticity of behaviour as being an evolutionary product itself): it presumes the limited behaviours examined within the laboratory are identical to those found without; and it presents the danger that the laws obtained in this arbitrary setting "may not be general, but peculiar to arbitrary events" (Seligman, 1972). The issue of the arbitrary nature of laboratory settings has been discussed by Seligman (1970 , 1972), in which he has argued that many of the premises of such research are tenuous and liable to major criticism (for an extended review of this topic see Seligman and Hager, 1972). Seligman's arguments are an extension of those of Breland & Breland, and complement those of Garcia *et al* (1966, 1968, 1972), Rozin and Kalat (1971), Bolles (1970, 1972), Brown and Jenkins (1968), Williams and Williams (1969), Falk (1968), Shettleworth (1972), Glickman and Schiff (1967) and Staddon and Simmelhag (1971).In the face of such wide-ranging research

and established results, the cherished amition to elucidate the generalised laws that govern behaviour seems to have had limited success, although Skinner still maintains that his approach has achieved these goals:

> "Reinforcers are chosen which are indeed reinforcing, either positively or negatively. In this way species differences in sensory equipment, and in possibly disruptive repetoires are minimised. The data then show an extraordinary uniformity over a wide range of species". (Skinner, 1969).

In restrospect the above quotation restates Skinners' 1959 position, indicating the Skinnerian approach has avoided examination of the critical issues cited, and that it does not accept species differences as being of sufficient merit to warrant specific research. Thus the contribution to the study of animal behaviour by Skinnerians rests largely on their enormous consideration of instrumental learning phenomena. It is difficult to deny the importance of research on processes such as schedules of reinforcement, discrimination learning, and the modifiability of behaviour, but, the apparent lack of generality of these findings to other phenomena, and their interactions with evolutionary influences makes much of this approach of limited value.

(4) A Changing emphasis.

In the light of the abovementioned criticisms of the traditional Skinnerian position, a major change in

the emphasis of Behaviourism has recently been suggested. Herrnstein, (1977) publishing in the *American Psychologist* has acknowledged the body of research that,

> ".....seem to be finding holes
> in the fabric of Skinnerianism".

His thesis concerns the way by which Skinnerian behaviourism has minimised the importance of four sources of variance in behaviour. He summarises these sources as;

(a) the varying susceptibilities of stimuli and responses to conditioning,

(b) the structure of stimulus and response classes,

(c) the inventory of drives, and

(d) the hedonic value of stimuli arising in behaviour.

Of these four points, he states:

> "All four depend on inborn motivational dynamics and all doubtless vary both within and across individuals in a species. Although behaviourists have from time to time recognised the existence of these factors, they have tended not to study how they feed into the quantitative laws of behaviour until quite recently. Behavioural engineering, resting on simplifying assumptions now shown inadequate, is bound to have trouble with these innate motivational dynamics as long as they are ignored, as the Brelands warned in 1961".

As Herrnstein is an ex-student and a contemporary colleague of Skinner's, his criticisms have had a strong effect upon behaviourists, provoking comment from no less than Skinner himself. The tone of Skinner's rebuttal is a curious mixture of denying that he made various statements, appeals to misinterpretation, and personal discredit, as is exemplified by the following excerpts from his paper in reply to Herrnstein:

> "When one has published nine books setting forth a scientific position, it is disconerting to find it misunderstood. To be misunderstood by a former student and present colleague is especially puzzling. Yet I do not recognize the views attributed to me by Professor Herrnstein (1977) in his explanation of a "rising tide of anti-Skinneriarism" (p593) in the evolution of behaviourism .....
>
> ..... Herrnstein (1977) finds *The Behaviour of Organisms* "too grandiose a title for a book about lever pressing by albino rats" (p596). It is. And so are Pavlov's *Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex* (a book about salivation in dogs) and Sherrington's *The Integrative Action of the Nervous System* (the bulk of which is about the simplest part of the nervous system

> and only in cats and dogs). And so, I suggest, is "The Evolution of Behaviourism", unless Herrnstein is contending that his own theory of drives and reinforcers is the wave of the future .... Herrnstein (1965) is co-editor of a distinguished source book in the history of psychology. In this particular case, proximity seems to have interfered with an objective evaluation". (Skinner, 1977).

Thus a new controversy appears to have arisen, but one that hardly seems likely to end in an unqualified success for Skinner's position in the light of the biologically-based evidence of recent research. Herrnstein's summary in his first 1977 paper ends with the statement,

> "Thus refined, behaviourism appears to merge with the main lines of ethology as a more complete science of behaviour than either one alone has been".

And yet, this comment merely echos the sentiments of the founder of behaviourism, made sixty three years earlier.

> "Without developing the subject further, it would seem obvious that there is no conflict between field work and laboratory work. The field is both the source of problems and the place where the laboratory solutions of these problems are tested". (J.B. Watson, 1914, P31).

(D) ETHOLOGY.

(1) Origins and emphases.

The first popular usage of the term 'ethology' was in the sense proposed by J.S. Mill to refer to the study of national and collective character (Jaynes, 1969); this usage remained in the English-speaking world until the 1900's. The now accepted usage arose out of the debates between Cuvier (a laboratory-oriented anti-evolutionist) and Geoffroy-Saint-Hilaire (an evolutionist and naturalist) in which Geoffroy-Saint-Hilaire (1859) used the term to refer to the "study of living things in their natural habitat". Although the naturalistic position was upheld and studied by a number of subsequent scholars, ethology as a specific discipline did not receive recognition until the 1940's, when Lorenz, Tinbergen, Baerends, and others used the word as a designative for their studies of animal behaviour in the natural environment. For an account of the historical origins of ethology see Jaynes, 1969.

Although the formal discipline of ethology is most readily identified with the writings of Konrad Lorenz and Niko Tinbergen, it has strong methodological and theoretical antecedants in the works of a number of biologically-oriented scientists who studied animal behaviour. In particular the works of Whitman (1899, 1919), Craig (1918), Spalding (1873), Selous (1905), Howard (1929), Huxley (1914), Von Uexküll (1921, 1937), and Verway (1930) have been cited as being of importance (Beer, 1963; Eibl-Eibesfeldt, 1972).

Ethology arose out of a reaction to the controlled

laboratory-based analyses of comparative experimental psychology on the one hand, and vitalistic (purposivistic) schools of European psychology (i.e. the *Gestaltist* approach) on the other. These origins are clearly summarised by Beer (1963, 1964), in which he notes:

> "By and large the psychologists had looked for behaviour, in animals, that conformed to the categories of learning patterns that had been worked out for humans, and had found little else; or they had dismissed the possibility of a satisfactory analysis of animals other than humans because such animals cannot introspect and tell us about their motives (e.g. Bierens de Haan, 1947). The physiologists, working at the level of simple reflexes, had generalised their results to the point of saying that all behaviour can be reduced to description or explanation in terms of simple stimulus-response connections - nervous links between specific receptors and specific effectors (e.g. Pavlov, 1927). It was largely a reaction to these teachings which established the existence of ethology .... The *Gestalt* people were convicted of vitalism, of retreating into mysticism before the

> limitations of a scientific analysis had been tested. The behaviourists were praised for their tough-mindedness but censured for their narrow-mindedness. If they had taken the trouble to accurately observe their animals, Lorenz claimed, they would have seen that much of the behaviour was spontaneous - not dependant on changes in the immediate external stimulus - and that reaction to a stimulus was rarely constant".

This statement summarises the main differences between ethology and other disciplines studying animal behaviour, and alludes to a most significant emphasis of ethology; the innate (instinctive) basis of behaviour. However, the key to the definition of this discipline is the emphasis upon the biological adaptiveness of behaviour; this strategy being clearly described by Beer (1963) as,

> "Properly to understand a piece of behaviour we have to appreciate its function in the life of the animal and its position in the whole behavioural repertoire of the animal. This necessitates study of the animal in its natural situation or in conditions that do not disguise the biological relevance of its behaviour".

It has been this emphasis upon the biological

relevance of behaviour that has led to the most widely accepted definition of ethology, namely.

> "the biological study of behaviour"
> (Tinbergen, 1963).

Tinbergen elaborated this definition further by adding,

> "By this I mean that the science is characterised by an observable phenomenon (behaviour or movement), and by a type of approach, a method of study (the biological method)".

He further noted that the major problems with which ethology concerns itself are, causation, survival value, evolution, and ontogeny. In presenting his viewpoint he qualified his arguments by stating that ethology is a science that was still in its infancy.

The relative newness of ethology as a formally recognised science can be assessed from the years of inception of the major ethological journals; *Zeitschrift für Tierpsychologie* (1937); *Behaviour* (1948); *British Journal for Animal Behaviour* (1953) (later to become *Animal Behaviour* in 1958); *Revue du Comportment Animal* (1966).

(2) The era of controversies.

Despite its' youth, ethology rapidly became involved in a series of major controversies, in which the ethologists challenged many of the cherished assumptions of behaviourism and comparative psychology. To a large extent it would seem that the ethological criticisms were

both valid and instrumental in bringing changes to these other approaches.

However, there was one major area where the ethological theories were shown in bad light, the Lorenz-Tinbergen models of instinct and motivation. This issue is well reviewed; for further consideration see Lorenz (1950); Tinbergen (1951); Beach (1955a, 1955b); Lehrman (1953, 1955); Schneirla (1956); Hinde (1956, 1959, 1960b). It may be speculated that the greatest significance of this controversy does not relate to the discrediting of the theoretical models, but rather to the value that was gained from the exposure to the scientific community of the ethological viewpoint, and the subsequent changes within ethology itself.

The work of the modern ethologists, up to the time of this controversy had been overshadowed by the personality and the enormous contribution of Konrad Lorenz. Such was his standing that Tinbergen (himself a great and meticulous ethologist) was moved, in a paper dedicated to Lorenz on the occasion of his sixtieth birthday, to bestow the title "father of modern ethology" upon Lorenz.

> "Lorenz can with justification be said to be the father of modern Ethology - even though he has had his forerunners; there is nothing amazing about every father having had a father" (Tinbergen, 1963).

However the challenge to Lorenz's and Tinbergen's formulations served to change the directions that ethological research was taking, and tended to dispell the

often dogmatic views that a few ethologists propounded. As Beer (1964) has commented of the rebuke Lorenz received from others who studied animal behaviour,

> "It is a nice irony that Lorenz, who claimed that it was possible (let alone an 'invariable law') for science 'to begin with pure observation, totally devoid of any preconceived theory and even working hypothesis' (Lorenz, 1950, 232), should be taken to task for selecting examples to demonstrate *a priori* principles and for failure to take account of the facts because of rigid and preconceived ideas (Lehrman, 1953)".

The general outcome of these controversies that befell ethology was a resynthesis of much of the theory, and the opening of a fruitfull dialogue with other approaches to animal behaviour.

(3) Contemporary features of ethology.

> In 1956, Hinde observed that,
> "It does not seem over-optimistic to suggest that ethology is now entering a period of rapid expansion - a process which may, however, require a thorough revision of some of the concepts which have grown up with it and seen it through its teething troubles".

Hinde has gone on to be the successful author of an authorative and comprehensive text entitled *"Animal Behaviour: A synthesis of ethology and comparative psychology"*. (1966, 1970), and has also co-edited a significant text on *"Constraints on Learning"* (Hinde and Stevenson-Hinde, 1973).

A number of books have appeared since 1966 that contain information of both an ethological and psychological nature, and all seem to achieve compatibility of theory and method. Examples of these include; *Mechanisms of Animal Behaviour* (Marler and Hamilton, 1966): *An Introduction to Animal Behaviour* (Manning, 1967), *Biological Boundaries of Learning* (Seligman and Hager, 1972); *Perspectives in Ethology* (Batson and Klopfer, 1973); *Development and Evolution of Behaviour* (Aronson, Tobach, Lehrman and Rosenblatt, 1970).

Furthermore, several papers have appeared in ethological and psychological journals that are a combination of both approaches, and indicate that the methodological rigour of psychology has been successfully grafted onto the evolutionary, adaptive and species-specific formulations of ethological theory. And the ethological subject areas (such as displacement behaviour, imprinting, and motivational causation) have been accepted into the general areas of interest to psychology.

The use of the observational technique has remained a strong methodological principle in ethology, but also has found favour in psychology. The application of powerful statistical analyses (a strong point in psychology) has found popularity amongst ethologists who have used some techniques with success in the analysis of complex patterns of behaviour. Examples of this can be found in papers by

Delius (1969); Perdeck (1960); Slater and Ollason (1972), Blurton-Jones (1968); and Hazlett and Bossert (1965). A further extension of statistical analysis is found in the work of D.J. McFarland who has applied the mathematical principles of electronic control - systems analysis to the causal factors relating to motivation (with hunger and thirst being the main focal topics), see McFarland (1971, 1974).

Clearly, the dialogue between comparative psychology and ethology has been of mutual benefit; while the inter-relationship between ethology and behaviourism has tended to develop at a slower pace, but seems to have found support over the last few years.

Schwartz (1974) in a review of Seligman and Hagers' *Biological Boundaries of Learning* (1972) has commented on the lack of mutual interchange between behaviourism (the experimental analysis of behaviour) and ethology, and has concluded:

> "This is not an optimal state of affairs. Ethology and the experimental analysis of behaviour are both fundamentally concerned with the origins of adaptive behaviour, and they should be able to contribute to each others' development. Fortunately, a rapidly growing set of laboratory observations over the last few years may provide the basis for a new dialogue between ethologists and psychologists".

The publication of a volume entitled *Naturalistic Viewpoints in Psychological Research* (Willems and Rausch (eds), 1969) is also significant in that it synthesises field observations of animals and humans with traditional psychological theory, and again emphasises the current harmony and fruitful advances that exist between these differing fields of study. Such evidence can only support a negative answer to a question raised by Beer (1964),

> "Is ethology losing its identify as
> a separate field of study then?"

(E) IN SUMMARY.

This essay has examined specific aspects of the main approaches to the study of animal behaviour. The contemporary student finds himself in an area of general acceptance of differing theoretical, methodological and philosopical attitudes to this science. In a manner akin to the "hybrid-vigour" familiar in genetics, a vast resynthesis has occurred over the last fifteen years, with a consequent benefit to knowledge.

The traditional approaches to animal behaviour have each received criticism, and have embodied change as a result. Comparative psychology was critisized for the poor biological basis to much of its theories, and its archaic view of evolution. Behaviourism has been accused of an unwarranted over-emphasis on too few species and an over-simplification of the experimental environment. Ethology, the most recently recognised discipline, was challenged over its poor methodological practices, and its

naive theorising. All three have benefited from this process of enquiry.

Many differences may never be truly settled; it is difficult to imagine a rapprochement between mechanism and vitalism, even though the expression of these mutually irreconcilable philosophies is of a minimal level in many of the approaches to animal behaviour. But it is reasonable to expect a further increase in the mutual exchange of knowledge from laboratory-based, and naturalistical-oriented research.

This has been eloquently summarised by Menzel (1969) in a discussion on his research into primate behaviour from both a laboratory and field perspective. In many respects his views echo the sentiments of Darwin, in that they emphasise that animal behaviour is inextricably woven into the process of evolution in all its guises.

> "Until we have discovered all that is involved in the existing animal-environment complex, it is impossible to determine to what extent we are breaking down this complex by bringing the animal to the laboratory. Insofar as a species is not restricted by ecological barriers it has either placed itself where we can find it, or is there because of an unbroken chain of ancestors, possibly for, millenia, were in related situation. These facts (or rather, the necessity for understanding what such facts entail) make the field a prime test situation

for anyone who takes biology and evolution seriously. Laboratory tests can be justified to the extent that they provide models of events that are found more generally and help us discover what in one way or another has been there all along; but attempts to invent new organisms, environments, or behaviours for their own sake would border on travesty. It is not our artifacts and inventions but nature's products that are the subject matter of animal psychology. (Menzel, 1969, p81).

R E F E R E N C E S

ADLER, H.E. and TOBACH, E. (1971) Comparative psychology is not dead. Amer. Psychol., 26, 857-858

ARONSON, L.R. TOBACH, E. LEHRMAN, D.S. and ROSENBLATT, J.S (eds) (1970) Development and evolution of behaviour: essays in memory of T.C. Schneirla. San Francisco: Freeman.

BASCOM, J. (1878) Comparative psychology or the growth and grades of intelligence. N.Y: Putman. (cited in Jaynes, 1969)

BATESON, P.P.G., and KLOPFER, P.H. (eds) (1973) Perspectives in ethology. N.Y. - Lond: Plenum Press.

BEACH, F.A. (1950) The snark was a boojum. Amer. Psych., 5, 115-124

BEACH, F.A. (1955a) The descent of instinct. Psychol. Rev., 62, 401-410

BEACH, F.A. (1955b) Ontongeny and living systems in: Schaffner, B (ed). Group processes, Macy Foundation Symp, 1954.

BEER, C.G. (1963,1964) Ethology - the zoologists approach to behaviour. Tuatara, pts 1 and 2. 11, 170-177 12, 16-39.

BIERENS DE HAAN, J.A. (1947) Animal psychology and the science of animal behaviour. Behav., 1, 71-80

BITTERMAN, M.E. (1965a) The evolution of intelligence. Scient. Amer., 212, 92-100.

BITTERMAN, M.E. (1965b) Phyletic differences in learning Amer. Psychol., 20, 396-410.

BLURTON-JONES, N.G. (1968) Observations and experiments on causation of threat displays of the Great Tit (Parus major). Anim. Behav. Monogr., 1, 75-158.

BOICE, R. (1971) On the fall of comparative psychology. Amer. Psychol., 26, 858-859.

BOLLES, R.C. (1970) Species-specific defense reactions and avoidance learning. Psych. Rev., 1970, 77, 32-48.

BOLLES, R.C. (1972) Reinforcement, expectancy and learning. Psych. Rev., 79, 394-409

BRELAND, K. and BRELAND, M. (1966) Animal Behaviour. Macmillan: N.Y.

BROWN, P.L., and JENKINS, H.M. (1968) Auto-shaping of the pigeon's key-peck. J. Exp. Anal. Behav., 1968., 11, 1-8.

CRAIG, W. (1918) Appetites and aversions as constituents of instincts. Biol. Bull., 34, 91-107.

DARWIN, C.R. (1871) The descent of man. London: Watts and Co., 1949.

DARWIN, C.R. (1872) The expression of the emotions in man and the animals. Chicago: Phoenix Books, 1965.

DELIUS, J.D. (1969) A stochastic analysis of maintenance behaviour in syklarks. Behav., 33, 137-171.

DEWSBURY, D.A. (1973) Comparative psychologists and their quest for uniformity. in. Tobach, E., Adler, H.E., and Adler, L.L. (eds). Comparative psychology at issue. 147-167.

DUKES, W.F. (1960) The snark revisited. Amer. Psychol., 15, 157.

DUNLAP, K. (1919) Are there any instincts? J. Abnorm. Soc. Psychol., 14, 307-311.

ESPINAS, A. (1877b) Des sociétés animals étude de psychologie comparée. Paris: Baillière. (cited in Jaynes 1969).

FLOURENS, P. (1861) De la raison, du génie, et de folie. Paris: Carnier frères. (cited in Jaynes 1969).

FLOURENS, P. (1864) Psychologie comparée. Paris: Carnier frères. (cited in Jaynes 1969).

GARCIA, J., and KOELLING, R.A. (1966) The relation of cue to consequence in avoidance learning. Psychon. Sci., 4, 123-124.

GARCIA, J., McGOWAN, B.K., ERVIN, F.R., and KOELLING, R.A. Cues - their relative effectiveness as a function of the reinforcer. Sci., 160, 794-795.

GARCIA, J., McGOWAN, B.K., and GREEN, K.F. (1972) Biological constraints on conditioning.in: BLACK, A.H., and PROKASY, W.F. (eds) Classical conditioning II: current research and theory. N.Y: Appleton-Century-Crofts.

GEOFFROY-SAINT-HILLAIRE, I. (1854-1862) Histoire naturelle générale. (3 vols). Paris: Masson. (cited in Jaynes, 1969).

GLICKMAN, S.E. and SCHIFF, B.B. (1967) A biological theory of reinforcement. Psychol. Rev. 74, 81-109.

GOTTLIER, G. (1976) Comparative Psychology. Amer Psychol., 31, 295-297.

GRAY, P.H. (1973) Comparative Psychology and ethology. in: Tobach, E., Adler, H.E., and Adler, L.L.(eds) Comparative psychology at issue 49-53.

HARLESS, M. (1971) On the demise of comparative psychology. Amer Psychol., 26, 1034.

HARLOW, H.F., GLUCK, J.P., and SUOMI, S.J. (1972) Generalization of behavioural data between non-human and human animals. Amer Psychol., 27, 709-716.

HAZELTT, B.A., and BOSSERT, W.H. (1965) A statistical analysis of the aggressive communications system of some hermit crabs. Anim. Behav., 13, 357-373.

HERRNSTEIN, R.J. (1967) Introduction. in: J.B. Watson, Behaviour: an introduction to comparative psychology. N.Y: Holt, Rhinehart and Winston (1967 reprinting).

HERRNSTEIN, R.J. (1977a) The evolution of behaviourism. Amer. Psychol., 32, 593-603.

HERRNSTEIN, R.J. (1977b) Doing what comes naturally: reply to Professor Skinner. Amer. Psychol., 32, 1013-16.

HERRNSTEIN, R.J. and BORING, E.G. (1965) A source book in the history of psychology. Cambridge, Mass: Harvard Univ. Press.

HINDE, R.A. (1956) Ethological models and the concept of drive. Brit. J. Philos. Sci., 6, 321-331.

HINDE, R.A. (1959) Unitary drives. Anim. Behav., 7, 130-141.

HINDE, R.A. (1960b) Energy models of motivation. in. S.E.B. Symp. XIV. Models and Analogues in Biology. Beament, J.W.L (ed). 199-213.

HINDE, R.A. (1966) Animal behaviour: A synthesis of ethology and comparative psychology (1st ed.) N.Y: McGraw-Hill.

HINDE, R.A. (1970) Animal behaviour: A synthesis of ethology and comparative psychology (2nd ed) N.Y: McGraw-Hill.

HINDE, R.A. and STEVENSON-HINDE, J. (eds) Constraints on Learning: Limitations and Predispositions. Academic Press: London, N.Y.

HODOS, W. and CAMPBELL, C.B.G. (1969) Scala naturae: Why there is no theory in comparative psychology. Psychol. Rev., 76, 337-350.

HOWARD, H.E. (1929) An introduction to the study of bird behaviour. Cambridge: Camb. Univ. Press.

HULL, C.L. (1945) The place of innate individual and species differences in a natural-science theory of behaviour. Psychol. Rev., 52, 55-60.

HUXLEY, J.S. (1914) The courtship habits of the great crested Grebe (Podiceps cristatus); with an addition to the theory of sexual selection. Proc. Zool. Soc. Lond., 2, 491-562

JAYNES, J. (1969) The historical origins of 'ethology' and 'comparative psychology' Anim. Behav., 17, 601-606.

JOLY, H. (1877) Psychologie comparée, l'homme et l'animal. Paris: Heurand Phil.
(cited in Jaynes, 1969).

KATZ, D. (1937) Animals and men: studies in comparative psychology. London: Longmans, Gree, & Co.

KUO, Z.Y. (1921) Giving up instincts in psychology. J. Phil., 18, 645-664.

KUO, Z.Y. (1924) A psychology without heredity. Psychol. Rev., 31, 427-448.

KUO, Z.Y. (1967) The dynamics of behaviour development: an epigenetic view. N.Y: Random House.

LEHRMAN, D.S. (1953) A critique of Konrad Lorenz's theory of instinctive behaviour. Quart. Rev. Biol., 28, 337-363.

LEHRMAN, D.S. (1955) On the organisation of material behaviour and the problems of instinct. in: L'instinct dans le comportement des animaux et de l'homme. (Masson et al eds) Paris: Singer-Polignac Foundation. 475-520.

LOCKHARD, R.B. (1968) The albino rat: a defensible choice or a bad habit? Amer. Psychol., 23, 734-742.

LOCKHARD, R.B. (1971) Reflections on the fall of comparative psychology: Is these a message for us all? Amer. Psychol., 1971, 26, 168-179.

LORENZ, K.Z. (1950) The comparative method of studying innate behaviour patterns. Symp. Soc. Exp. Biol., 4, 221-268.

LORENZ, K.Z. (1965) Evolution and modification of behaviour Chicago: Chicago Univ. Press

MAIER, N.R.F. and SCHNEIRLA, T.C. (1935) Principles of animal psychology. N.Y: McGraw-Hill

MANNING, A. (1967) An introduction to animal behaviour London: Edward Arnold Ltd.

MARLER, P and HAMILTON, W.J. (1966) Mechanisms of animal behaviour N.Y: J.Wiley and sons.

McDOUGALL, W. (1923) Outline of psychology N.Y: Scribner.

McFarland, D.J. (1971) Feedback mechanisms in animal behaviour. London: Academic Press.

McFARLAND, D.J. (ed) (1974) Motivational control systems analysis London: Academic Press.

MENZEL, E.W. (1969) Naturalistic and experimental approaches to primate behaviour. in: WILLEMS, E.P., and Raush, H.L. (eds) Naturalistic viewpoints in psychological research.

MORGAN, C.L. (1894) An introduction to comparative psychology. London: Walter Scott.

MORGAN, C.L. (1904) Introduction to comparative psychology (2nd ed) London: Scott.

MOSS, F.A. (ed) (1942) Comparative psychology (rev. ed) N.Y: Prentice-Hall.

PAVLOV, I.P. (1927) Conditioned reflexes Oxford Univ. Press: London.

PERDECK, A.C. (1960) Observations of the reproductive behaviour of the Great Skua or Bonxie, Stercorarius Skua, in Shetland. Ardea, 48, 111-136.

PLOTKIN, H.C. (1971) On behavioural universals: or, is comparative psychology quite dead? Amer. Psychol., 26, 1034-1035.

RATNER, S.C., and DENNY, M.R. (1964) Comparative psychology. Homewood, I11: Dorsey.

RATNER, S.C. (1972) Comparative psychology: some distinctions from animal behaviour. The Psychol. Rec. 22, 433-440.

ROMANES, G.J. (1883) Animal intelligence. N.Y: Appleton.

ROMANES, G.J. (1884) Mental evolution in animals N.Y: Appleton.

ROMANES, G.J. (1910) Animal intelligence London: Routledge.

ROZIN, P., and KALAT, J.W. (1971) Specific hungers and poison avoidance as adaptive specializations of learning. Psychol. Rev., 78, 459-486.

RUSSELL, R.W. (1973) On the definition of comparative psychology. in: Tobach, E., Adler, H.E., and Adler, L.L. (eds). Comparative psychology at issue. 54-57.

SCHNEIRLA, T.C. (1956) Interrelationship of the 'innate' and 'acquired' in instinctive behaviour. in: L'instinct dans le comportement des animaux et de l'homme. (Masson et al eds) Paris: Singer-Polognac Foundation. 387-432

SCHNEIRLA, T.C. (1966) Behavioural development and comparative psychology. Quart. Rev Biol., 41, 283-302.

SCHWARTZ, B. (1974) On going back to nature: A review of Seligman and Hagers' Biological boundaries of learning. J. Exp. Anal. Behav., 21, 183-198.

SCOTT, J.P. (1958) Animal behaviour. Chicago: Univ. Chicago Press.

SCOTT, J.P. (1973) The organization of comparative psychology. in: Tobach, E., Adler, H.E., and Adler, L.L. (eds) Comparative psychology at issue. 7-40.

SELIGMAN, M.E.P. (1970) On the generality of the laws of learning. Psych. Rev., 1970, 77, 406-418.

SELIGMAN, M.E.D., and HAGER, J.L. (1972) Biological boundaries of learning N.Y: Appleton - Century-Crofts.

SELOUS, E. (1905) Observations tending to throw light on the question of sexual selection in birds, including a day-to-day diary on the breeding habits of the ruff (Machetes pugnax). Zoologist. (4) 10 and 11.
(cited in Beer, 1964).

SHETTLEWORTH, S. (1972) Constraints on learning. Adv. Study Behav., 4, 1-68.

SIMPSON, G.G. (1958) The study of evolution: methods and present states of theory. in: Roe, A., and Simpson, G. G. (eds) Behaviour and evolution New Haven: Yale Univ. Press.

SKINNER, B.F. (1938) The Behaviour of Organisms. Appleton. Century-Crofts: N.Y.

SKINNER, B.F. (1959) A case history in scientific method in: Koch, S. (ed) Psychology-a study of a science. N.Y: McGraw-Hill. Vol 2.

SKINNER, B.F. (1969) Contingencies of reinforcement: a theoretical analysis. N.Y: Appleton-Century-Crofts.

SKINNER, B.F. (1977) Herrnstein and the evolution of behaviourism. Amer. Psychol. 32, 1006-1012.

SLATER, P.J.B., and OLLASON, J.C. (1972) The temporal pattern of behaviour in isolated male Zebra Finches: transition matrices. Behav., 42, 248-269.

SPALDING, D.A. (1873) Instinct, with original observations on young animals. Reprinted in Brit. J. Anim. Behav., 2, 2-11

SPENCER, H. (1875) Comparative psychology. Anthrop. J., 5, 301-316
(cited in Jaynes, 1969).

STADDON, J.E.R., and SIMMELHAG, V.L. (1971) The superstition experiment: a reexamination of its implications for the principles of adaptive behaviour. Psych. Rev., 1971, 278 3-43.

STONE, C.P. (ed) (1951) Comparative psychology. (3rd ed) Englewood Cliffs, N.J: Prentice-Hall.

THORNDIKE, E.L. (1911) Animal intelligence. N.Y: Macmillian.

THORPE, W.H. (1956) Learning and instinct in animals. London: Methuen.

THORPE, W.H. (1973) Is there a comparative psychology? in: Tobach, E., Adler, H.E., and Adler, L.L. Comparative psychology at issue. 89-112.

TINBERGEN, N. (1951) The study of instinct. Oxford: Clarendon Press.

TINBERGEN, N. (1963) On aims and methods of ethology Z. Tierpsychol., 20, 410-424.

TISSOT, J. (1878) Psychologie comparée. Paris: A Maresq âine
(cited in Jaynes, 1969).

TOBACH, E., ADLER, H.E., and ADLER, L.L. (eds) Comparative psychology at issue. Annals, N.Y. Acad. Scie., 223.

TOLMAN, E.C. (1932) Purposive behaviour in animals and man. N.Y: Appleton-Century- Crofts.

UEXKÜLL, J. von (1921) Umwelt und Innenwelt der Tiere. (2nd ed) Berlin:

UEXKÜLL, J. von. (1937) Umweltsforschung. Z. Tierpsychol., 1, 33-34.

VERWAY, J. (1930) Die Paarungsbiologie des Fischreihers. Zool. Jahrb. Allgem. Zool. Physiol., 48, 1-120.

VIGNOLI, T. (1877) Di psyicologia comparate. Milano: Dumolard.
(cited in Jaynes, 1969).

WARDEN, C.J. (1927) The historical development of comparative psychology. Psychol. Rev., 34, 57-85, and 135-168.

WARDEN, C.J., JENKINS, T.N. and WARNER, L.H. (1936) Comparative psychology: a comprehensive treatise. (3 vols) N.Y: The Ronald Press Coy.

WASHBURN, M.F. (1936) The animal mind. N.Y: Macmillan Coy.

WATERS, R.H., RETHLINGSHAFER, D.A., and CALDWELL, W.E. (eds)(1960) Principles of comparative psychology. N.Y: McGraw-Hill.

WATSON, J.B. (1914) Behaviour: an introduction to comparative psychology. N.Y: Holt; (reprinted 1967).

WHALEN, R.E. (1961) Comparative psychology. Amer. Psychol. 16, 84.

WHITMAN, C.O. (1899) Animal behaviour. Biol-Lect. Marine Biol. Lab Woods' Hole, Mass. 1899.
(cited in Beer 1964)

WHITMAN, C.O. (1919) The behaviour of pigeons. Carnegie Inst. Wash Publ. 275- 1-161. (cited in Beer, 1964).

WILCOX, J. (1972) Comparative psychology lives on under an assumed name - Psychogenetics! Amer. Psychol., 27. 531-538.

WILLEMS, E.P., and RAUSH, H.L. (eds) (1969) Naturalistic viewpoints in psychological research. N.Y: Holt, Rhinehart and Winston.

WILLIAMS, D.R., and WILLIAMS, H. (1969) Auto-maintenance in the pigeon: Sustained pecking despite contingent non-reinforcement. J. Exp. Anal. Behav., 1969, 12, 511-520.

YEAGER, D.L. (1973) Comparative psychology? Amer. Psychol., 28, 181-184.

YERKES, R.M. (1913) Comparative psychology: a question of definitions. J. Philos., 10, 580-582.

ZEIGLER, H.P. (1973) The problem of comparison in comparative psychology. in: Tobach, E., Adler, H.E., and Adler, L.L. (eds). Comparative psychology at issue. 126-134.

A P P E N D I X T W O

OF RATS AND FERRETS.

The experimental work presented in this thesis has been based upon two species of mammal, the laboratory rat, and the ferret. Each species is an example of a defined ecological type, one being an omnivore, and the other a carnivore. The literature on the biology and behaviour of the rat is vast, since this species is probably the most popular of all laboratory animals, a situation that has led to a major criticism of Psychology because of an overdependence upon it in research (see Appendix One). The ferret has not been widely used, although it has a long history of domestication, being a popular game catching animal. This chapter will selectively examine aspects of the biology of each species, and review some of the relevant literature pertaining to each.

The Rat (*Rattus norvegicus var. albinus*).

The first recorded use of the albino rat in experimental research was by Steward in 1898 (Lockhard, 1968). From this time the use of the rat has increased, so that the scientific information about its behaviour probably exceeds that of any other species (with the possible exception of man). The close association with

the affairs of man has been a feature of the rat from an early time and emphasizes an important feature of ORDER *Rodentia* as a whole, namely their success at adapting to, and exploiting fully, different environmental conditions. Apart from a global distribution in which they have colonised continents and remote islands, rats have adapted their lives to survive well in human communities. A key feature of the *Rodentia* is their high breeding rate, which enables them to displace competing species by sheer weight of numbers. Typifying the importance accorded to the *Rodentia*, the following statement exemplifies many found in texts on evolutionary biology:

> "The criteria of evolutionary success are various. We like to think of ourselves as the most successful of all animals, for in our own way we rule the world. Yet we are but a single species, and the great dominance we now enjoy has been a development of the last thousand years. As contrasted with the evolutionary success of man, or of the order primates, or of any other mammalian order, the rodents have been supremely successful during most of the Cenozoic times. If the range of adaptive radiation, the numbers of species are a criteria of success in evolution, the rodents far outshine all other

> mammals ..... All these considerations point up the fact that the rodents and lagomorphs have been extraordinarily successful animals during the last fifty or sixty million years. From the evolutionary viewpoint these animals represent the climax of mammalian success." (Colbert, 1961).

The rat is a member of the Superfamily *Muroidea*, which is comprised of the families *Cricetidea* and *Muridea;* the laboratory rat belonging to the latter. The terms "rat" and "mouse" are more a function of size, than of taxonomy, as both families contain species referred to by these names (Dewsbury, 1974). The *Muridea* emerged in the late *Miocene* era, approximately 15 million years ago.

Apart from being a relative newcomer to the *Rodentia* the rat differs from the majority of the rodents in that it is an omnivore, rather than a herbivore. Rats have been known to occupy a variety of habitats, ranging from semi-aquatic burrows to the transportation systems of man; it has been this latter habitat that has provided them with a major vector in their spread over the globe. Within these habitats they capitalise and exploit any available food source. Although they are voracious eaters, they also exhibit caution when encountering novel food in a familiar environment, a factor that protects their survival when attempts to

eradicate them with poisoned bait are made. This caution of new food has been termed "neophobia" (Barnett, 1963), although this term also refers to the general avoidance of novel objects in their environment. In these situations, wild rats show a reluctance to approach a "new" object for several days, and when contact is made, it is initially brief.

There are two types of wild rat, the brown or Norway rat (*Rattus norvegicus Berkenhout*), and the black or house rat (*Rattus rattus Linnaeus*). Of these two species, the brown rat is the more common, although the two species can occupy a common geographical environment, e.g. in dwellings *norvegicus* may live in the floor and sewer level, whilst *rattus* may reside in the walls and ceilings (Lockhard, (1968). These two species may rarely intermate, but do not develop viable foetuses. In the laboratory situation *rattus* is rarely used, as it does not easily domesticate.

Both *norvegicus* and *rattus* originated in Asia, and were unknown in Europe until the time of the Crusades, when travel and commerce assisted in their spread. *Rattus* was the first to appear in Europe, rapidly becoming a common pest, and through the fleas it carried, transmitted bubonic plague. Although *norvegicus* was a later arrival, by 1790 it had also become a major pest. Because rats were a nuisance, they were caught in great numbers, and used in the sport of rat-baiting. Because of the popularity of this sport and the difficulty in maintaining a supply of rats, attempts were made to breed these animals in captivity. (Richter, 1954). Consequent to breeding in captivity, the occasional albino mutant was

kept out for novelty and show purposes, and this led to the domestication of the rat.

Because of its tractability, and the ease with it bred in captivity, the rat was an obvious choice as a laboratory animal. Lockhard (1968) records the history of their experimental use as beginning with Philipeaux (1856), and that the first psychological research with the rat was by Steward (1898), Kline (1899), and Small (1900). The first authoritative book on the rat was by Donaldson (1915, revised in 1924), in which the results of his research over the years 1893-1924 were summarised. It was from Donaldson's colony in Chicago that Watson obtained his subjects for his early experiments. Another important researcher was Crampe, who conducted breeding experiments between 1877 and 1885. This research later led to the discovery of 3 mutant genes that were transmitted by albino females when crossed with wild males; these being c (albino), a (nonagouti), and h (hooded). The nonagouti (or black mutation) is accompanied by gentler behaviour, and most albino strains possess this gene, although the albino gene prevents its expression. Hooded rats are not markedly different from *albinus*, although they appear to be more reactive to their environment.

The result of this continued research on the rat has culminated in a vast library of knowledge on every aspect of behaviour of these animals, with their learning abilities being most represented. This research is well summarised in a number of books and scientific journals, and in particular:

The Journal of Comparative and Physiological Psychology (previously titled *The Journal of Comparative Psychology*), *The Journal of the Experimental Analysis of Behaviour*, *The rat: Data and reference tables* (Donaldson, 1924), *Maternal Behaviour in the Rat* (Wiesner and Sheard, 1933), *Handbook of Psychological Research on the Rat* (Munn, 1950), *The Rat: A Study in Behaviour* (Barnett, 1963), and *The Albino Rat: A Defensible Choice or a Bad Habit?* (Lockhard, 1968).

A major criticism of the rat as a laboratory animal stems from the fact that the albino variety is a far different animal from its wild counterpart, from which it was derived. While wild rats are able to breed with the albino varieties, they are markedly different in their behaviour. Lockhard (1968) considers these differences, which may be summarised as follows:

Wild *norvegicus* differ from *albinus* in a number of ways including; they are more excitable, they have heavier skeletons, suparenal glands, testes, and ovaries; they have a larger brain and spinal cord; the social organisation of the wild *norvegicus* is complex and well developed whilst that of *albinus* is immature and poorly developed; *albinus* has lost a number of the sterotyped behaviours common to *norvegicus*: the fits and convulsions that certain strains of *albinus* exhibit are unknown in *norvegicus*: *norvegicus* has a greater range and degree of vocalisation which is poorly developed in *albinus*: the activity of *norvegicus* is markedly greater under conditions of food deprivation than it is in *albinus*; muricide is common in *norvegicus* and rare in *albinus*; and neophobia is very reduced in *albinus* while it is a significant feature of wild *norvegicus*.

Apart from the abovementioned criticisms, Lockhard points out that the population of *albinus* itself is not a homogeneous sample, and therefore the argument that it is a standardised subject is invalid.

> In summary, *albinus* is not one rat, but many, depending upon the source. Types popular with psychologists are heterogenous, with wide individual differences, in contrast to recognised strains designated by combinations of capital letters and numbers. The statistical properties of a colony's gene pool change with time, making last decade's data out of date - from animals no longer existent. And *albinus* is not *norvegicus;* it is rapidly evolving, and it is only a matter of time until it is recognised as a separate species. It is hardly a random sample from the population of "organisms"; it is more like a commercial product.(Lockhard, 1968)

Further criticism comes from Beach (1950), who challenges the view that the use of the rat is purely an arbitrary choice and suggests that what has happened to experimental psychology is that it has become a "science of rat learning".

> "To sum up, I suggest that the current popularity of rats as experimental subjects is in large measure of the

> consequence of historical accident,
> Certainly it is not the result of
> systematic examination of the avail-
> able species with subsequent selection
> of this particular animal as the one
> best suited to the problems under study".
> (Beach, 1950).

Another cogent criticism of the use of the laboratory rat is that the rigidly controlled world of the animal laboratory alters the behaviour of the subjects, and if they come from stock with many generations of such living, then they are different animals from their wild counterparts. A number of proponents have suggested that this may be true, including: Richter (1959), Barnett (1963), Kavanau (1964), Lockhard (1968), and Wagner (1971). The latter author demonstrated that the sugar preferences of wild kangaroo rats completely reversed over a period of months in which they adjusted to laboratory living, so that the subjects demonstrated sugar preferences that "were qualitatively similar to those of other laboratory-bred rodents". He concluded that care is needed in generalising from one species to another, and within species if some consideration is not given to what laboratory living does to an animal.

> "It is suggested that laboratory
> living produces a different animal
> and that this implies the need for
> the exercise of extreme caution in
> reporting general laws of motivation,
> learning, or development based on
> studies of the behaviour of laboratory

> bred or reared animals and also for caution in making too few or too brief examinations of the behaviour which may often change due to adaptation or sensitization to the experimental situation". (Wagner, 1971).

An assumption of this criticism is that only the less dominant and adaptable animals have been caught in the first stages of domestication, and consequently the gene pool is based upon less active members of the total population: i.e. domestication has militated towards degeneracy, both through a biased gene pool, and because the environment does not provide those selective pressures necessary for the development of behavioural variability. This assumption of domestication equated with degeneracy is strongly argued by Lockhard (1968, 1971).

However, Boice (1972) has challenged this assumption, with its attendant corollary that degeneracy reflects a decrease in learning ability. He presents evidence that suggests that "the domesticated rat is a better learner than his wild progenitor" (Boice, 1968; 1970) and concludes:

> "The results, which must be considered preliminary, are supportive of the notion that domestication in the Norway rat has induced an adaptive fitness rather than degeneration." (Boice, 1972).

Thus, it may be speculated that the adaptiveness that aided the rats' spread across the world, may also be operating within the laboratory environment to promote

domesticity, and accordingly provide science with a good model for the study of domestication. As Boice (1972) notes:

> "It may be, for example, that the domesticated rat is more fit than its progenitor for research (Tinbergen, 1965; Dobzhansky, 1967) and more appropriate for generalisation to domesticated man, assuming man is domesticated (Richter, 1959; Eibl-Eibesfeldt, 1970)."

Clearly this issue is unresolved, but irrespective of whatever theoretical and experimental directions behavioural research may tend towards in the future, it seems unlikely that the contribution to the subject matter of science by the rat as an experimental subject can be overlooked. The numerous criticisms of rat-oriented psychology notwithstanding, it is unlikely that the use of this animal will diminish in the forseeable near future.

The Ferret (*Mustela putorius hybrid*).

The ferret belongs to the family *Mustelidae*, genera *Mustela* (to which group the weasel (*Mustela nivalis*) and the stoat (*Mustela ermina*) also belong). These species are representative of typical primitive carnivores, as Ewer (1973) observes,

> "The *Mustelinae* include the most predacious species and, in relation to their size, the weasels and stoats

> are killers as formidable and efficient as the larger Felidae." (p.171).

The ferret differs from the stoat and weasel in size (being longer and substantially heavier), and is easily domesticated (whereas the stoat and weasel do not take well to captivity). The ferret has a long history of domestication, its contact with man dating from at least the time of the Greeks.

> "Aristotle mentions that polecats are easily tamed but there is no suggestion of true domestication. Thomson (1951) regarded the earliest mention of ferrets as being in Strabo's *Geographica*, dating back to the beginning of the Christian era. Strabo describes how rabbits can easily be killed by using an animal believed to be a ferret to flush them from their burrows." (Ewer, 1973, P. 398).

Because of their value in controlling the rabbit population ferrets, weasels, and stoats were liberated in New Zealand over the period from 1882 to 1897 (Marshall, 1963). This introduction of mustelids was deemed necessary to control the rapidly burgeoning rabbit population in New Zealand, as there were no natural predators to control them, and the rabbit had rapidly become a serious pest to the newly developed pastures and grazing lands. Due to the urgency associated with the need for their introduction, the ferret was imported from

Great Britain (but the stock may have included specimens from the European Continent, as well as true polecats, *Mustela furo Linnaeus;* see Marshall, 1963 for further discussion). As a consequence the feral population of ferrets in New Zealand are probably a hybrid group of *Mustela putorius*, *Mustela furo*, and possibly *Putorius putorius*. Since this issue has not been clarified, the ferrets used in this research will simply be referred to as *Mustela putorius hybrid*, in recognition of the potential variations in their genetic make-up.

Despite the fact that ferrets have had a considerable association with man, they have not achieved popularity as a subject in behavioural research. In many respects this is unfortunate, as they present minimal difficulties in terms of husbandry, are small and easily handled and are sturdy and able to tolerate experimental manipulations (e.g. food deprivation, injection of pharmacological agents).

The bulk of research on the ferret has been concerned with their predatory behaviour patterns, social development, exploratory behaviour, and their performance in learning situations.

The predatory behaviour in a number of carnivores is closely linked to play behaviour when the animals are young, since the predatory behaviour has a large learned component.

> "In the acquisition of adaptive behaviour, carnivores must go through a stage of education, as Ewer (1971) calls it, in which they learn to make a living for

> themselves. The end result must be behaviour which is adaptable in a variety of situations, therefore the "economical way to achieve this is to restrict the endogenous components to something approaching the minimum required to make the animal act in such a way as to ensure that it will learn the rest ....." Without risk of serious injury from the prey (Ewer, 1971). A great part of the learning that perfects predatory behaviour is rapid; Leyhausen (1965) compares it to imprinting phenomena, e.g. the ease with which the killing bite "clicks into place", after one or very few successes, quite unlike the typical learning curve, which describes how an animal learns what it is not especially programmed to do (Ewer, 1971)." (Eaton, 1972).

In the case of the ferret, the predatory "killing bite" has to be learned, and this learning is facilitated by the opportunity to engage in play with litter-mates (Eibl-Eibesfeldt, 1955c, 1963, 1975). The predatory neck-biting behaviour also has importance in mating behaviour, where an inexperienced isolation-reared male has to learn this response by trial and error through the females defensive reactions (Eibl-Eibesfeldt, 1963). The

patterns and development of aggressive play, aggression, and social play are described in papers by Poole (1966, 1972), Lazar and Beckhorn (1974), and in Eibl-Eibesfeldt (1975).

Attack behaviour towards prey appears to be partially in response to movement (Eibl-Eibesfeldt, 1975), and partially to smell (Räber, 1944; Apfelbach, 1973a, 1973b). These references indicate that the ferret has to learn both the smell of the prey, and the mode of attack. In feral animals it would seem that smell takes precedence over movement as an attack eliciting stimulus, as Pollard (1968) has cited Ward (personal communication) as observing,

> "We have often seen ferrets hunting by day, moving from one burrow to the next, and although rabbits have been sitting nearly above ground, they have taken little notice of them and concentrated entirely on hunting down burrows."

This observation is consistent with the findings of Pollard and Lewis (1968) in which they noted that ferrets' performances in the Hebb-Williams maze were similar to the behaviour of nocturnal rats and possums in this setting,

> "Suggesting that they made little use of available visual cues" (Pollard and Lewis, 1968).

This finding does not imply that ferrets are poor visual learners, since Pollard, Beale, Lysons and Preston (1967) had found that ferrets were able to learn visual discrimination problems in a Yerkes discrimination

apparatus, although their performances were different from those of hooded rats in several respects; and the authors concluded,

> "that some ferrets may sustain a figure-ground reversal of some stimuli but that this is by no means characteristic of visual organisation in the species."

Another aspect of visual and learning behaviour to be examined has been the ferrets' responses to novel situations (i.e. their exploratory behaviour). Hughes (1965b) examined the responses to the ferrets in a spontaneous alternation situation, finding that the subjects engaged in spontaneous alternation by entering the alternate arm of a Y-maze to the arm they intially entered. He also found ferrets would respond to brightness changes in a similar situation (Hughes, 1964, 1965b, 1967). These findings were extended by Eastment and Hughes (1968) with an observation that ferrets will enter "the more visually complex of 2 Y-maze arms more often during a 60-sec period."

In general there does not appear to be much research on other aspects of the behaviour of ferrets, possibly because several of the usual psychological manipulations (in the area of learning research) have been unsuccessful with this species (e.g. Pollard and Lewis, 1968, comment on the difficulties experienced when trying to teach these animals to emit sustained bar-pressing behaviour: see Chapter Six for further discussion).

Given the degree by which the adult behaviour of ferrets is influenced by learning experiences in their

early life, through play behaviour and manipulation within their environment (e.g. aggressive, predatory, and mating behaviour), these animals would seem ideally suited to "deprivation-type" experiments where isolation from conspecifics and other species at various points of development are imposed upon the subject. Such studies would be of benefit to the understanding of the ontogeny of behaviour and the role of species-specific behaviours. Also the ferret would seem to be suitable as a subject for studies examining mechanisms of adaptation, as proposed by Hodos and Campbell (1969). These authors state of this approach:

> "This method is based on the study of living animals, selected because they possess differing of specialization (adaptation) with respect to some particular characteristic such as development of sense organs or central nervous system, the amount of postnatal care given to offspring, complexity of courtship patterns etc."

Because of their size, robustness, and general reactivity to their environment, ferrets would seem to be an ideal subject for laboratory studies of the carnivorous mode of existence.

R E F E R E N C E S

APFELBACH, R. (1973a) Olfactory sign stimulus for prey selection in polecats (Putorius putorius. L.) Z. Tierspsychol., 33, 270-273.

APFELBACH, R. (1973b) Woran erkennt ein Raubtier seine Beute? Umschau 73, heft 15, 453-457.

BARNETT, S.A. (1963) The rat: a study in behaviour. Chicago: Aldine.

BEACH, F.A. (1950) The snark was a boojum. Amer. Psychol., 1950,5, 115-124.

BOICE, R. (1968) Conditioned licking in wild F_1 and domestic Norway rats. J. Comp. Physiol. Psychol., 1968,66, 796-799 .

BOICE, R. (1970) The effect of domestication on avoidance learning in the Norway rat. Psychon. Sci., 18, 13-14.

BOICE, R. (1972) Some behavioural tests of domestication in Norway rats. Behav., 42, 198-231.

COLBERT, E.H. (1961) Evolution of the Vertebrates. (rev. ed.) N.Y: John Wiley and Sons.

CRAMPE, H. (1877) Kreuzungen Zwischen Wanderraten verschiedener Farbe. Landwirthschaftliche Jahrbücher, 1877, 6, 385-395 (cited in Lockhard, 1968).

DARWIN, C.R. (1871) The descent of man. London: Watts and Co., 1949.

DARWIN, C.R. (1872) The expression of the emotions in man and the animals. Chicago: Phoenix Books, 1965.

DEWSBURY, D.A. (1974) The use of muroid rodents in the psychology laboratory. Behav. Res. Meth and Instrum., 6, 301-308.

DOBZHANSKY, T. (1967) Mankind evolving. New Haven: Yale Univ. Press.

DONALDSON, H.H. (1924) The rat: Data and reference tables. Philadelphia: Wistar Institute Memoir No. 6, 1924 (cited in Lockhard, 1968).

EASTMENT, A.M. and HUGHES, R.N. (1967) Reactions of ferret - polecat hybrids to complexity and change. Percept. Mot. Skills., 26, 935-938.

EATON, R.L. (1972) Predatory and feeding behaviour in adult lions: the deprivation experiment. Z. Tierspsychol., 31, 461-473.

EIBL-EIBESFELDT, I. (1955c) Sexualverhalten und Eiablage beim Alpenmolch. Wiss. Film c698 Gottingen (inst. wiss. Film)
(cited in EIBL-EIBESFELDT, 1975).

EIBL-EIBESFELDT, I. (1963) Angeborenes und Erworbenes im Verhalten einiger säuger. Z. Tierpsychol., 20 705-754
(cited in EIBL-EIBESFELDT, 1975).

EIBL-EIBESFELDT, I. (1970) Ethology. (1st ed) N.Y: Holt, Rhinehart and Winston.

EIBL-EIBESFELDT, I. (1975) Ethology. (2nd ed) N.Y: Holt, Rhinehart and Winston.

EWER, R.F. (1971) Care and education of the young in Felidae. paper presented at: Intern. Symp. oh Ecology, Behaviour and Conservation of the World's Cats. Laguna Hills, California, March, 1971
(cited in Eaton, 1972).

EWER, R.F. (1973) The carnivores. London: Weidenfeld and Nicolson.

HODOS, W. and CAMPBELL, C.B.G. (1969) Scala naturae: why there is no theory in comparative psychology. Psychol. Rev., 76, 337-350.

HUGHES, R.N. (1964) Responses by the ferret to stimulus change. Brit. J. Psychol., 55, 463-468.

HUGHES, R.N. (1965b) Spontaneous alternation and response to stimulus change in the ferret. J. Comp. Physiol. 1965, 60, 149-150.

HUGHES, R.N. (1967) Effects of intertrial confinement and brightness change on ferret alternation behaviour. Psychol. Rep., 20, 679-681.

KAVANAU, J.L. (1964) Behaviour: confinement, adaptation, and compulsory regimes in laboratory studies. Scie, 1964, 143, 490.

KLINE, L.W. (1899) Methods in animal psychology. Amer. J. Psychol., 10, 256-279
(cited in Lockhard, 1968).

LAZAR, J.W. and BECKHORN, G.D. (1974) Social play or the development of social behaviour in ferrets (Mustela putcrius)? Amer. Zool., 14, 405-414.

LEYHAUSEN, P. (1965) Über die Funktion der relativen Stimmungshierachie. Z. Tierpsychol., 22, 412-494.

LOCKHARD, R.B. (1968) The albino rat: a defensible choice or a bad habit? Amer. Psychol., 23, 734-742.

LOCKHARD, R.B. (1971) Reflections on the fall of comparative psychology: Is there a message for us all? Amer. Psychol., 1971, 26, 168-179

MARSHALL, W.H. (1963) The ecology of mustelids in New Zealand. N.Z.D.S.I.R. publication, Information series No 38.

MUNN, N.L. (1950) Handbook of psychological research on the rat. Boston: Houghton-Mifflin.

PHILLIPEAUX, J.M. (1856) Note sur l'extirpation des capsules survenales chez les rats albinos (Mus rattus) Comptes Rendus de la Academie des Sciences (Paris), 1856,43 904-906
(cited in Lockhard 1968).

POLLARD, J.S., BEALE, I.L., LYSONS, A.M., and PRESTON, A.C. (1967) Visual discrimination in the ferret. Percept. Mot Skills., 24, 279-282.

POLLARD, J.S. and LEWIS, R.F.V. (1968) Ferrets do learn mazes. J. Biol Psychol., 11, 40-43.

POOLE, T.B. (1966) Aggressive play in polecats. Symp. Zool. Soc Lond., 18, 23-44.

POOLE, T.B. (1972) Diadic interactions between pairs of male polecats (Mustela furo and Mustela furo x M. putorius hybrids) under standardised environmental conditions during the breeding season. Z. Tierpsychol., 30, 45-58.

RÄUBER, H. (1944) Versuch zur Ermittlung des Beuteschemas an einem Hausmarder (Martes foina) und einem Iltis (Putorius putorius). Revue Suisse de Zoologie, 51, 293-332.

RICHTER, C.P. (1954) The effects of domestication and selection on the behaviour of the Norway rat. J. National Cancer, Institute., 15, 727-738 (cited Lockhard, 1968).

RICHTER, C.P. (1959) Rats, man and the welfare state. Amer. Psychol., 1959, 14, 18-28.

SCOTT, J.P. (1973) The organization of comparative psychology. in: Tobach, E., ADLER, H.E. and ADLER, L.L. (eds). Annals N.Y. Acad. Scie., 1973, 223 pp 7-40.

SIMPSON, G.G. (1958) The study of evolution: methods and present status of theory. in: ROE, A., and SIMPSON, G.G. (eds) Behaviour and evolution. New Haven: Yale Univ. Press.

SMALL, W.S. (1900) An experimental study of the mental processes of the rat. Amer. J. Psychol., 1900, 11 133-165
(cited in Lockhard, 1968).

STEWARD, C.C. (1898) Variations in daily activity produced by alcohol and by changes in barometric pressure and diet, with a description of recording methods. Amer. J. Physiol., 1898, 1, 40-56
(cited in Lockhard, 1968).

THOMSON, A.P.D. (1951) A history of the ferret. J. Hist. Med. Sci., 6, 471-480.

TINBERGEN, N. (1965) Animal Behaviour. N.Y: Time Inc.

WAGNER, M.W. (1971) Laboratory living produces a different animal. Psychologische Beiträge, 1971, 13, 79-88

WEISNER, B.F. and SHEARD, N.M. (1933) Maternal behaviour in the rat. Edinburgh: Oliver and Boyd.

A P P E N D I X T H R E E

A DESCRIPTION OF THE EXPERIMENTAL APPARATUS USED.

The research was conducted in three basic experimental chambers that differed in dimensions to suit the species used. These chambers were made out of 1cm wooden ply for simplicity and ease of modification, and were adaptable to accommodate various pieces of equipment as the research required.

The initial research using rats was carried out in *Rat Chamber 1.*, but this chamber was replaced in later experiments by *Rat Chamber 2.*, when it was found to have inadequate ventilation, lighting, and drainage for the copious urine produced in polydipsic sessions. All research with ferrets was conducted in the *Ferret Chamber* which was found to be suited to the experimental programme.

Control of food delivery was determined by a solid state electronic control console, which provided accurate timing of delivery. This console also controlled a number of subsidiary functions; in particular, the duration and timing of signals warning of food delivery, the transformation of electrical signals from the various sensing devices (e.g. the drinkometers and the running wheel) to mechanical signals on the event recorders and counters, and the mechanical recording of the number of food-portions delivered over the experimental session.

All experimental situations were provided with white noise generators that masked sounds from outside the laboratory.

(A) The Experimental Layout.

The control console and the Rat Chambers were located in the same room, along with the various recording devices, counters, white-noise generator, and maintenance equipment; while the Ferret Chamber was sited in an adjacent room, with the necessary control wiring running to and from it through a hole in the wall. A floor plan of the layout is given in Fig. A3.1. The control console permitted the simultaneous operation of both the Ferret and Rat Chambers, without any disturbance to the subjects in either apparatus. Both rooms were centrally heated with an ambient temperature of 23 $\pm$ 2^{o}c being recorded.

The control console was a locally assembled solid state device marketed by PYE Ltd., Auckland, and sold under the name of Pye High Level Industrial Control Equipment. This sytem operated on a 230V AC power supply, with an internal logic power system of $\pm$ 40V DC. The timing devices in this system had an error specification of $\pm$ 5%. The timing and control functions of this system were found to be reliable over the period that this equipment was used.

The white noise generator used was a Lafayette Instrument Coy. Model 15011., with a speaker in each research room that masked extraneous noise.

Two Esterline-Angus Event recorders were used for the mechanical recording of various events.

Because of the variety of control, sensing, and recording equipment used, each with differing power requirements, several electro-mechanical relays were built into the system to permit simultaneous operation.

(B) Rat Chamber 1.

This chamber measured 38cm x 38cm x 25.5cm high, and was constructed of 1cm wooden ply, with a clear perspex door on the front wall. The floor was painted gloss black, while the walls and roof were painted matt light grey. A polythene food delivery tube of 5.6cm diameter entered into the chamber through a hole in the roof, and was butted into a similar hole in the floor. The floor of the food tube was of opaque perspex, with a light beneath it to serve as a signal for the delivery of food.

Internal lighting was provided by a 230V 60W lamp sited on the roof, which spread diffuse light into the chamber through a piece of opaque perspex in the roof.

A side view of the apparatus is given in Fig. A3.2, and shows the siting of a hole in the side wall for the spout that was attached to the water reservoir and connected to the drinkometer. In order to provide the drinkometer with an earthing contact, a steel mesh grid was attached to the floor in the vicinity of this spout. A plan view of the chamber is given in Fig. A3.3, in which the spatial relationship between the food tube and

the water-spout is made clearer. The minimum distance between these two was 28.5 cm. The water reservoir was graduated to record 30 mls in 1 ml units, and provided a reserve of water that could be recorded by measuring with a pipette. The drinkometer used in this experimental situation was a Grason-Stadler Model E4690 A1/A2.

Food was delivered from a Davis Universal Feeder (Model 310), which had a 36 portion capacity (requiring refilling during the course of the experimental session). This feeder operated on the brush-sweep principle, which permitted the use of a wide variety of foods, although only two types of food were used with the rats.

The maximum temperature reached in this chamber after one hour was 29^{o}c. The delivery of food was signalled by the onset of the light under the food-tube, and a simultaneous buzzer signal, both of which lasted a duration of 3 seconds. The buzzer was attached to the under floor of the chamber and was audible over the white noise.

(C) Rat Chamber 2.

This chamber measured 61cm x 38cm x 38cm high, and was constructed out of 1 cm wooden ply, painted light grey on all surfaces. The front wall was made out of transparent perspex and permitted a clear view of the subject. The floor had a steel mesh grid over most of its surface to permit the use of drinkometers at several points in the chamber and to facilitate drainage. A perspex food delivery tube of 8.0cm diameter projected

through a hole in the roof to a receptacle in the floor (a similar arrangement to that in *Rat Chamber 1*), and the floor of this food receptacle was made of a piece of opaque perspex (covering a signal light as in the other apparatus). A side view of this chamber is given in Fig. A3.4 and shows the arrangement for lighting through the roof. Internal lighting was provided by a 230V 22W circular fluorescent lamp. A plan view of this chamber is given in Fig. A3.5 and shows the positioning of holes in the wall for water-spouts used in the polydipsia experiments. This chamber had the capacity for the simultaneous operation of two drinkometers, during which occasions the Grason-Stadler drinkometer was supplemented with a Lafayette Model 5808 unit. Each drinkometer provided a record on the Esterline-Angus recorder, as well as having a mechanical counter to record total licks made on each spout.

(D) Ferret Chamber.

The ferret chamber was made out of 1cm ply, and measured 60cm x 60cm x 38cm high. The floor was painted gloss black (to facilitate cleaning) while the walls were painted matt grey. The door was made out of clear perspex. Selected parts of the floor were covered with steel mesh to permit the use of a drinkometer. Food was delivered via a vertical perspex tube measuring 8.0cm in diameter and of similar structure to those used in the rat chambers. The floor of the food receptacle was made of opaque perspex.

A side view of the chamber is given in Fig. A3.6 and shows the siting of a circular entrance to the activity wheel. A plan view of the basic chamber is given in Fig. A3.7. Because of the large size of this chamber it was not necessary to provide any internal lighting.

As was discussed in Chapter 5, the design of the activity wheel presented a number of problems as it was required to be sturdy, but not heavy, since the rotational inertia of a heavy structure would make it difficult for the animals to stop. However, a light structure proved vulnerable to activities of the ferrets, and was subject to several modifications before it was found to be satisfactory.

The wheel measured 75cm's in diameter, with an internal treadle width of 15cm's. Rotation was effected via a bearing fixed to the centre of the wheel, and this revolved around a brass axle fixed to the roof of the experimental chamber. The wheel was constructed of aluminium diamond mesh, with a fine wire-gauze flooring provided on the treadle floor to prevent the subjects' claws being caught in the mesh. Revolutions of the wheel were recorded through a fixed magnet on the wheel causing a depression of a reed-switch sited on the roof of the experimental chamber. The reed-switch was wired into an automatic counter. A side view of the wheel in relation to the experimental chamber is given in Fig. A3.8, and a plan view in Fig. A3.9.

Figure A3.1: Plan view of the Experimental Situation.

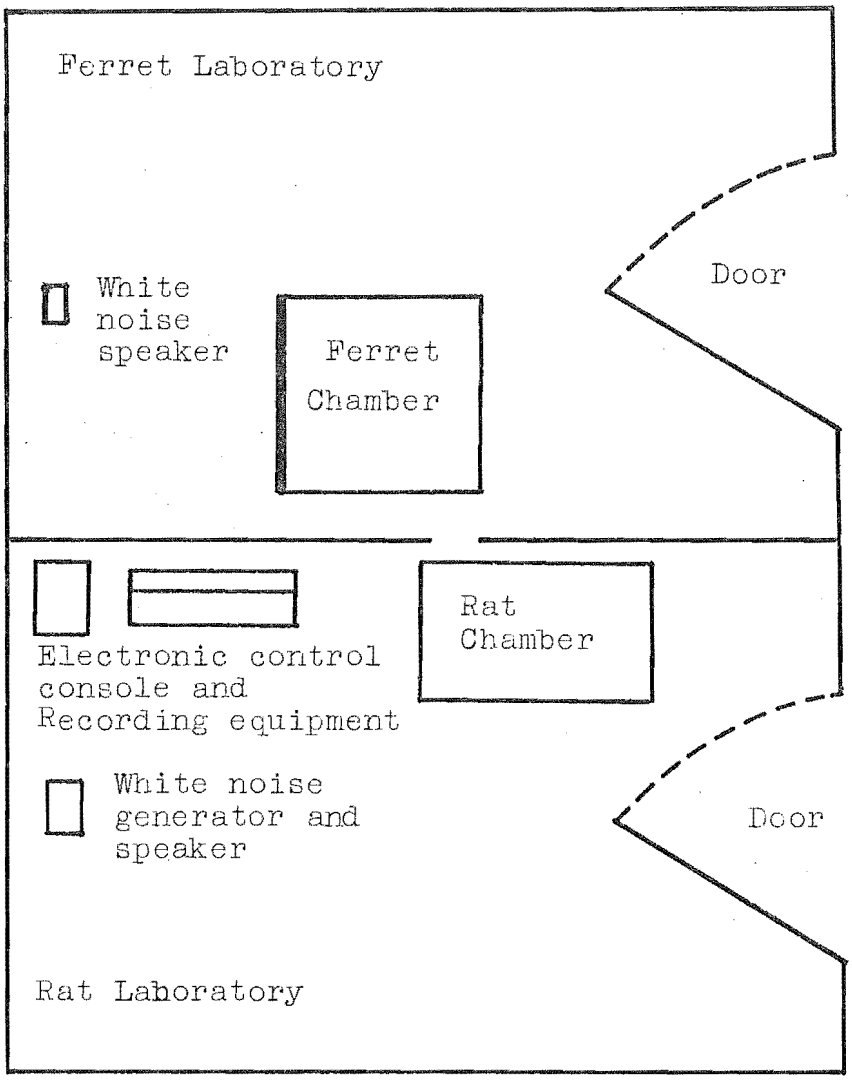


Figure A3.2: Rat Chamber 1, a Side View.

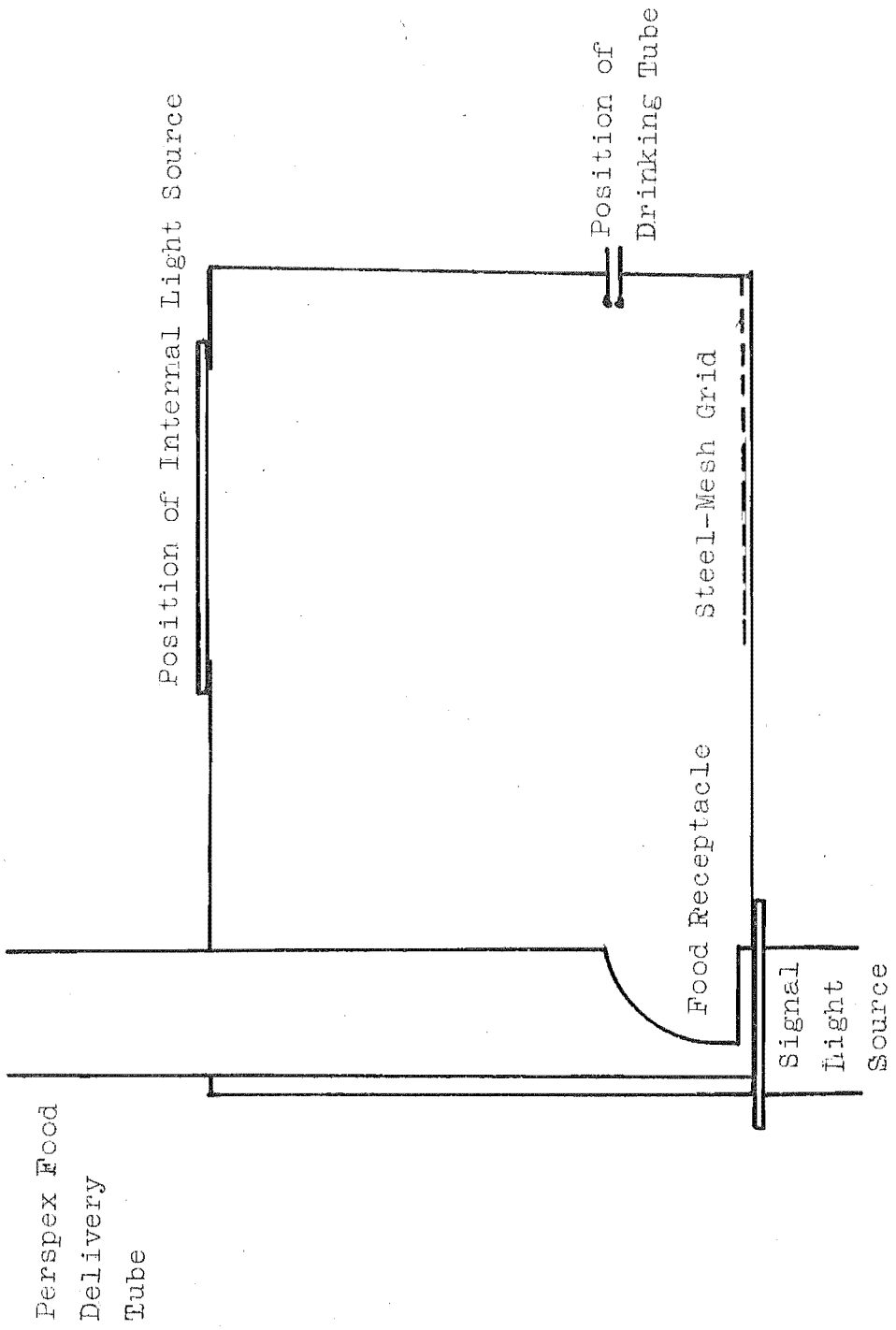


Figure A3.3: Rat Chamber 1, a Plan View.

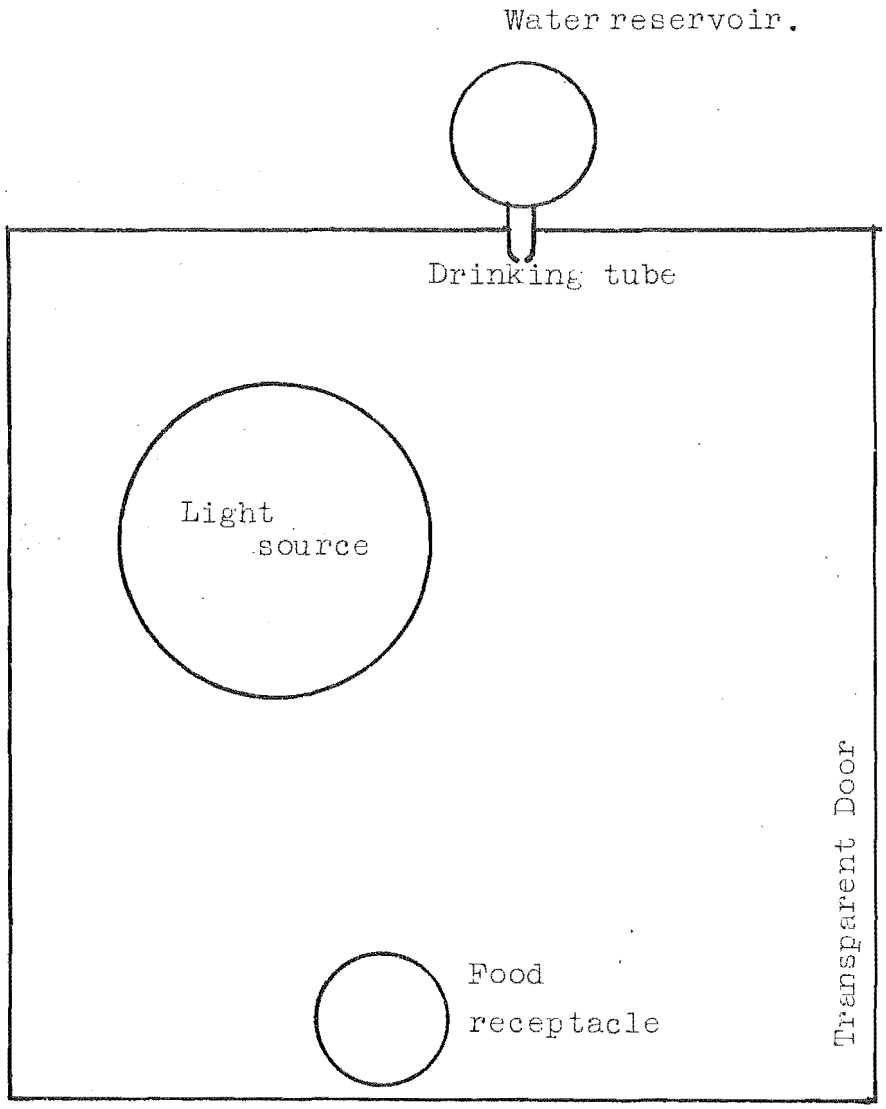


Figure A3.4: Rat Chamber 2, a Side View

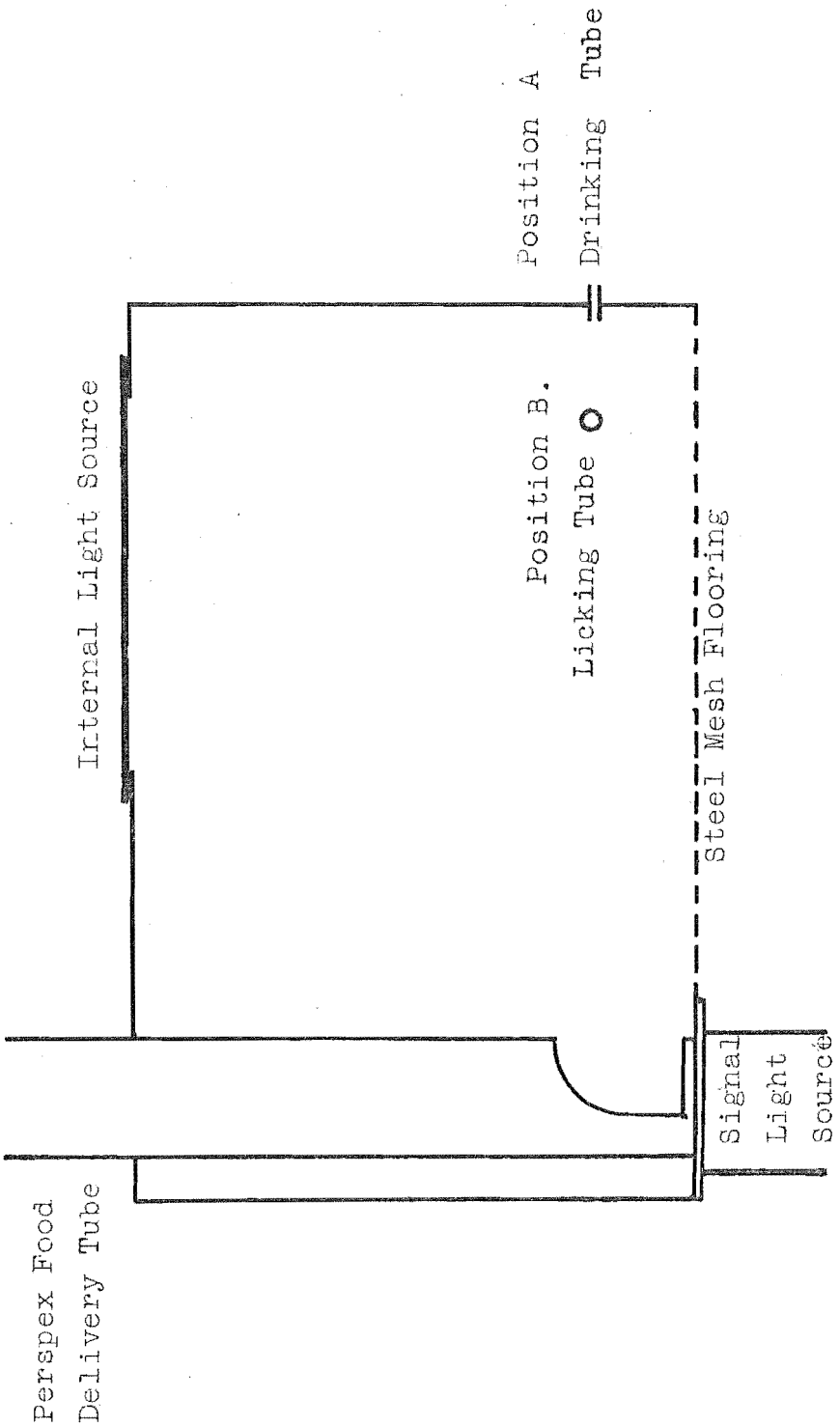


Figure A3.5: Rat Chamber 2, a Plan View

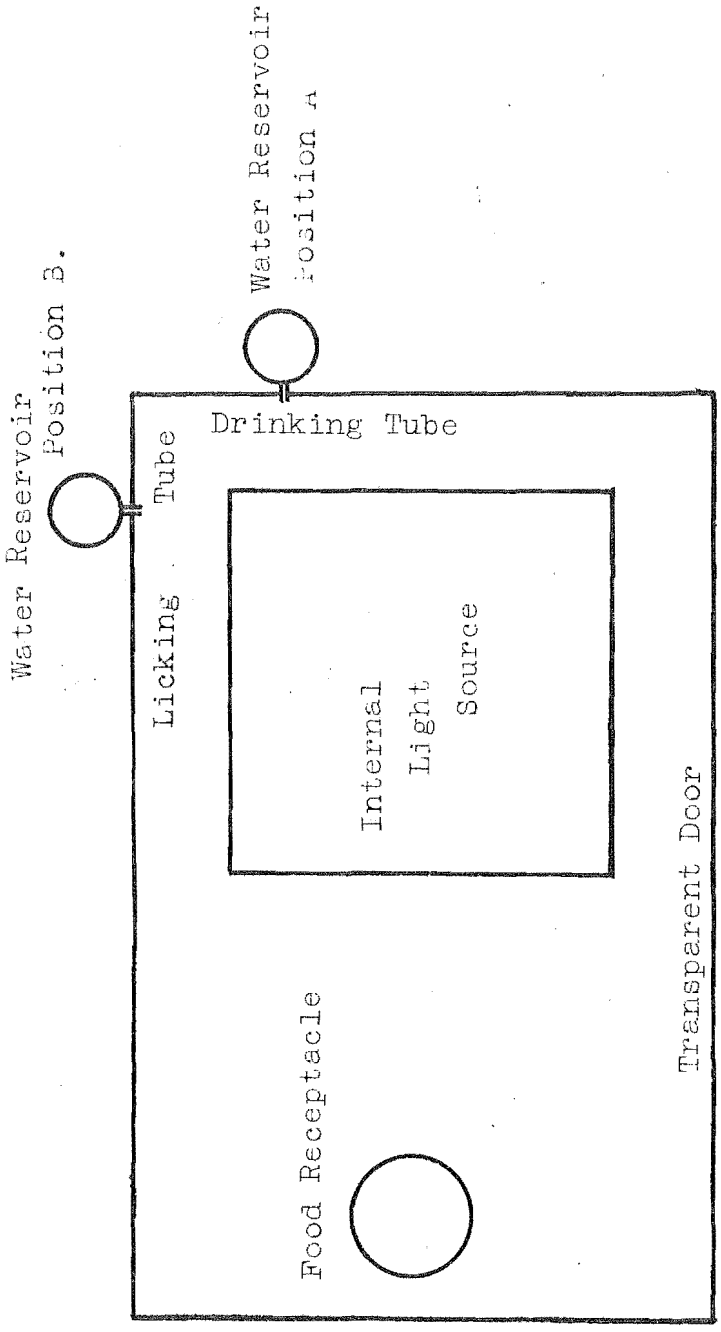


Figure A3.6: Ferret Chamber, a Side View

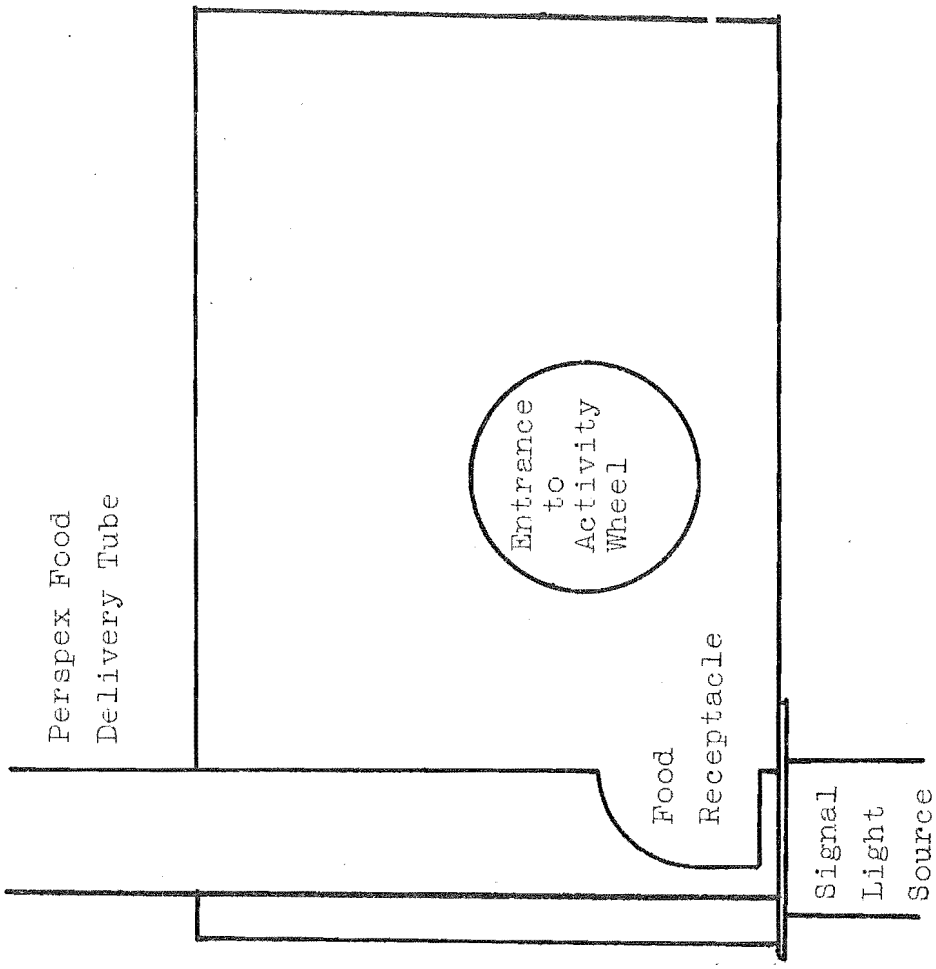


Figure A3.7: Ferret Chamber, a Plan View

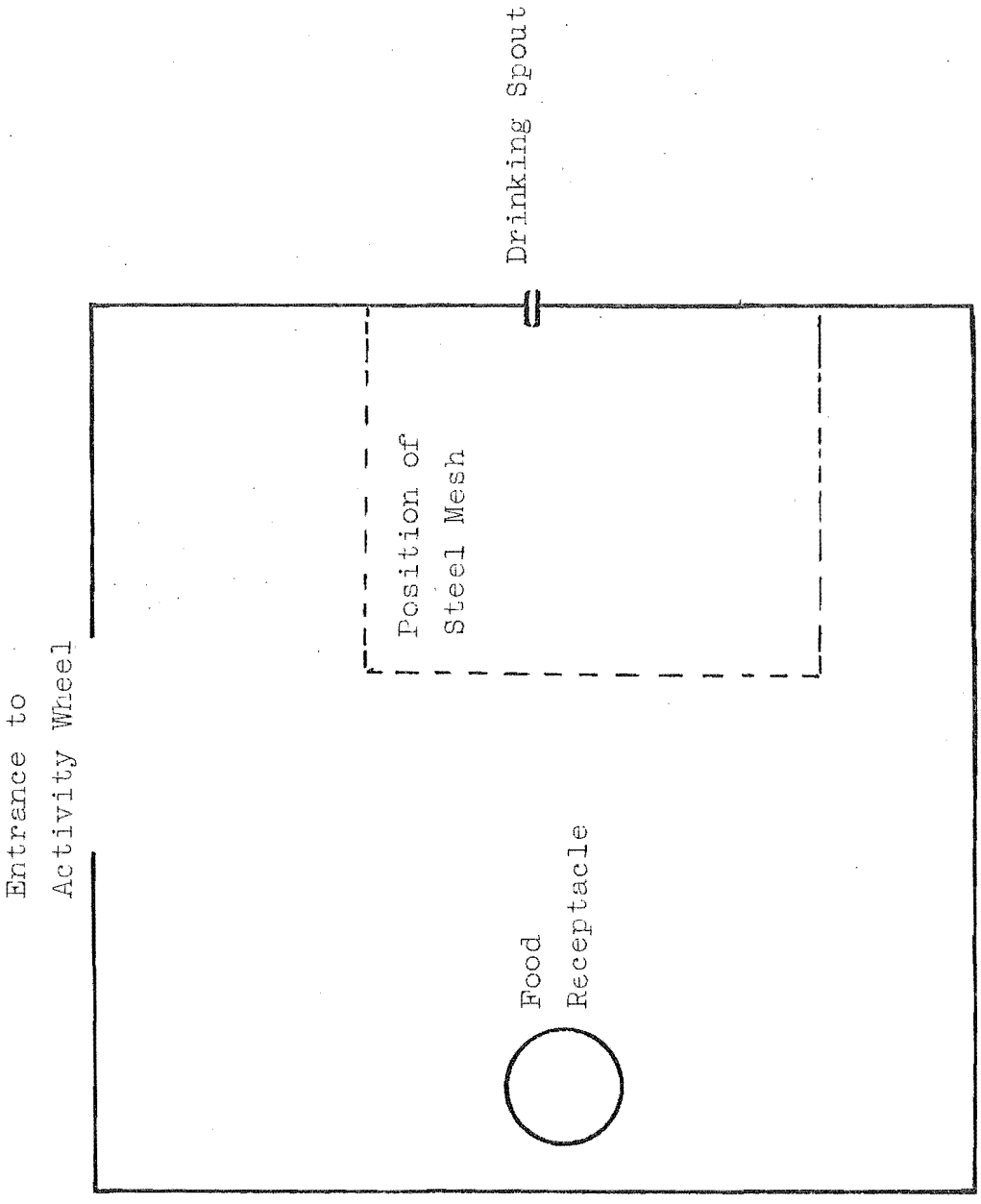


Figure A3.8: Ferret Activity Wheel, a Side View.

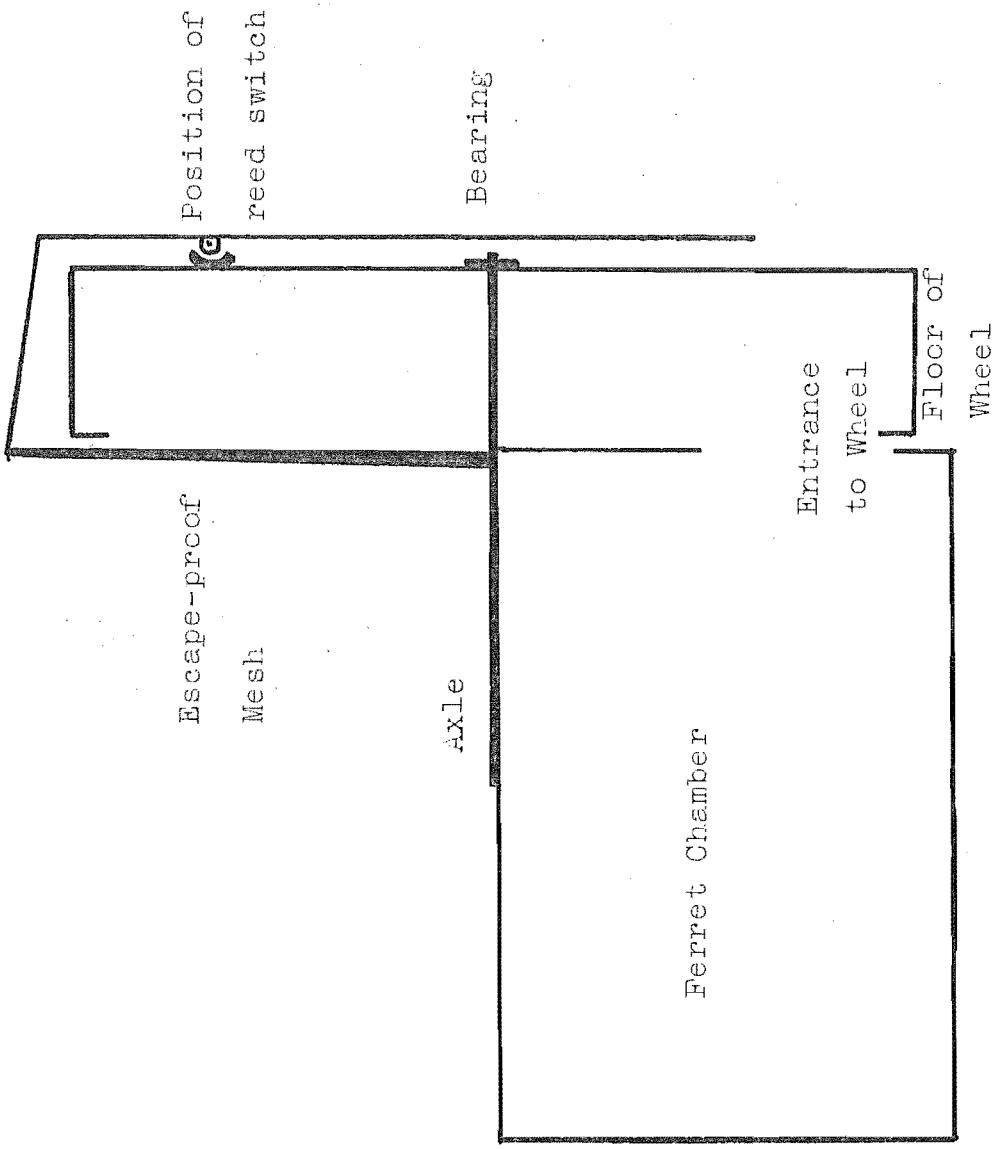
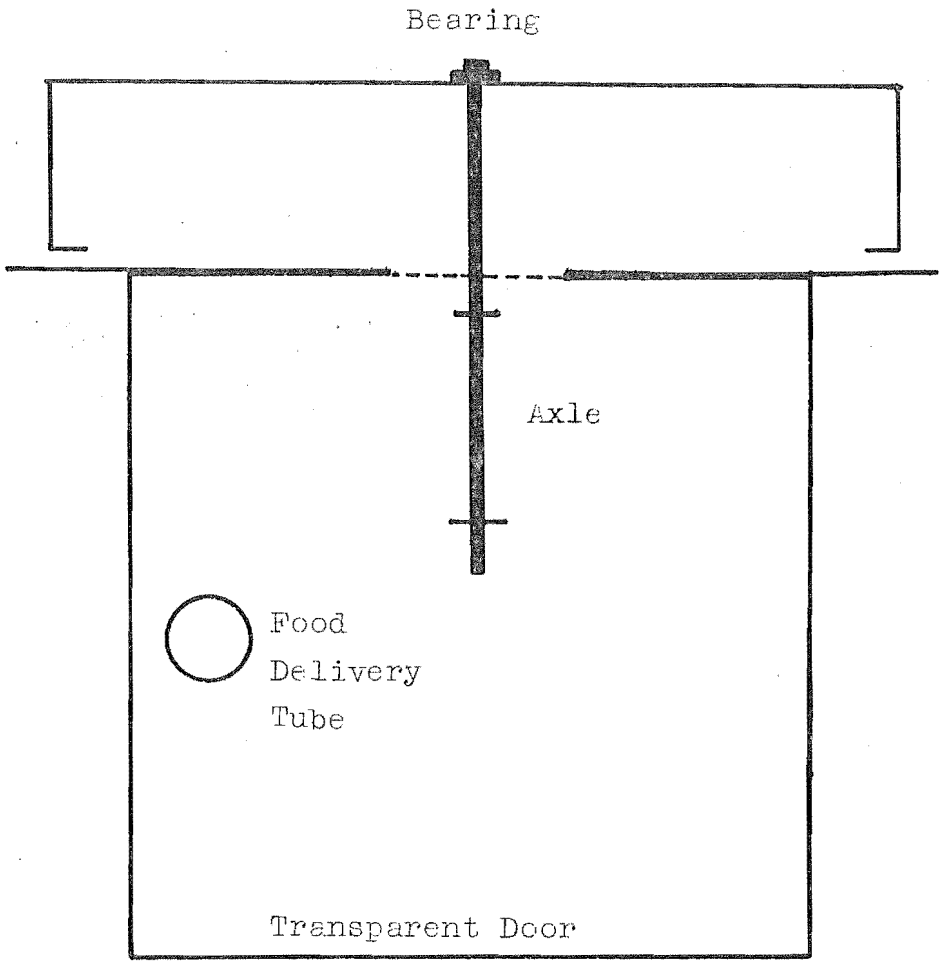


Figure A3.9: Ferret Activity Wheel, a Plan View.



A P P E N D I X F O U R

THE HOUSING AND DIET OF THE SUBJECTS.

The rats and ferrets used in this research were bred in the animal house of the Department of Psychology. These animals were under the care of two technicians who were responsible for the breeding and general maintenance of the animal colony. The experimental subjects cited in this thesis were the responsibility of the author who attended to their feeding, and controlled their food and water intake, as determined by the experimental requirements at that time (eg. maintenance at 80% free-feeding weight).

(A) Housing and Maintenance of the Rats.

The rats used in this research were New Zealand Black/White Strain originally from stock bred at the Medical School at Otago University. The animals were housed in same sex groups until required for experimentation, when they were put into individual metal cages measuring 18cm x 19.5cm x 18cm high. These cages had a flooring of wood shavings which were changed weekly. The cages were located on metal racks in two rat rooms which were maintained at a temperature of approximately $23^{o}C$. A reversed light/dark cycle (12 hours light

starting at 7:00 pm and going on to 12 hours dark at 7:00 am) operated in these rooms throughout the year.

The rats were normally maintained on ad libitum food and water, unless they were being deprived for some experimental manipulation. The basic diet comprised pellets of food sold under the name of T.V.L. Rat Diet. (manufactured by Archer and Sons, Rangiora, N.Z., to a recipe supplied by T.V.L. Laboratories, Christchurch, N.Z.). A breakdown of this diet is given in Table A4.1. This diet was supplemented once a week by additional food in the form of bread, raw vegetable, and dog sausage, such that a balanced diet was maintained. Subjects on food deprivation were given some of this supplement whenever it was possible, and also received an occasional Vitamin Supplement in their drinking water.

The general health of the rat colony was good, with a low mortality rate being recorded. Those deaths recorded were usually young rats found to be suffering from a congenital hydrocephaly (approx 5% of all births). One periodic disease which did affect research was a form of respiratory infection which gave symptoms similar to catarrh, and which adversely affected the performance of one rat in an isolated portion of one polydipsia experiment. It was thought to be due, in part, to dust from the wood shavings, and was found to be controlled by administering "Tylan" (tylosin tartrate) to the animal's drinking water. Because the animals received regular handling from birth, emotional behaviour was minimised, and the subjects found to be agreeably tame over the course of experimentation.

(B) Housing and Maintenance of the Ferrets.

The ferrets were bred in the animal house from feral stock which were originally acquired in 1961. The policy of mating local stock with feral animals caught during the year has been followed ever since, so that the established gene pool has been supplemented regularly in order to guarantee viable stock. As a result of this breeding policy, and with the husbandry experience gained over this period, a very high success rate has been achieved with the breeding of these animals, enabling the Department to become an established supplier of ferrets to other places.

The animals were kept in mixed sex groups of about 6 - 10 animals, and were separated into single sex groups in mid-August when the females showed signs of coming into oestrus. This separation of the sexes continued until the end of January when the breeding season ended. It was possible to group-house males over the mating season provided there were no females in close proximity to their cages; during this period instances of aggressive behaviour increased. When group-housed, the animals were kept in large cages which had an inside compartment (with a quantity of straw for bedding), and an outside compartment (with a layer of straw on the floor). When the animals were individually housed, they were put in either one of the above mentioned cages or in a wooden cage measuring 51cm x 136cm x 51cm high located inside the animal house in a well lit and ventilated passageway. These cages were cleaned out weekly and plentiful amounts of straw

and sawdust replaced, as these animals otherwise posed a considerable sanitation problem.

The animals were fed daily, and received 30-40 grams of a locally produced Dog Sausage 'BARKO' (manufactured by Criterion Animal Food, Ashburton, N.Z.) A table of contents of this food is given in Table A4.2. Water was available on an *ad libitum* basis from bottles attached to the cages, with a glass drinking spout projecting into the cage. This method avoided the spillages found to be so common when dishes of water were placed in the cages. The animals also received 15-20 mls of milk every second day, and mutton bones once a week. Castor oil was given monthly.

Because of the need to house these animals in open spaces it was not possible to institute an artificial daylight regime, so that natural lighting was used. Although these animals are most active at dusk and dawn, this was not found to influence their suitability as subjects in any way. Due to the variety of diet, and to the husbandary techniques used, there was a very low mortality rate amongst the ferret colony. The main source of illness stemmed from infected lesions arising as a result of aggressive behaviour between group housed animals. These lesions occasionally produced abcesses which were liable to cause paralysis if not treated. The standard treatment was a course of 'Penstrep' (procaine penicyllin and streptomycin), which proved effective if given as a series of intra-muscular injections over a week. Due to their being handled regularly from birth, these animals were extremely tractable, and could be safely

handled by the experimenter without gloves.

(C) An Analysis of the Experimental Session Foods.

(i) Rat Foods:

Initially, wheat was used in the pilot study, but its use was discontinued in the ensuing experiments because of the availability of a standardised commercially-prepared alternative. This product was sold under the name of Animal Food Pellets (manufactured by Sterling Pharmaceuticals Ltd., Auckland, N.Z.). A breakdown of these pellets is given in Table 4.3 Each pellet weighed 40 mg, and they were found to be stable over long periods (not becoming stale). They appeared to be highly palatable to the rats.

(ii) Ferret Foods:

In the first experiment with ferrets pieces of raw mutton were used as food portions. These portions were cut into pieces of 1.0 - 1.5 gms weight, and were dipped in cod-liver oil to prevent their drying out (and consequently adhering to the food dispenser). Although the ferrets avidly consumed these portions, it was found that the oil was producing a problem with stickiness in the food delivery equipment, which required constant cleaning of the apparatus. Also, it was difficult to control for portion size, moisture content, and meat content (i.e. gristle and fat were often present). Thus portions of 'Barko' dog sausage were substituted, and were found to be most suitable, as constant portion sizes could be obtained easily, the food was of a lower moisture content than raw

meat, and did not require cod-liver oil to prevent drying and adhering. The ferrets indicated an immediate acceptance of this food.

TABLE A4.1

Composition of T.V.L. Rat Diet.

Meat and Bone Meal.	12.00%
Lucerne Meal.	5.00%
Linseed Meal.	5.00%
Molasses.	2.75%
Butter Milk Powder.	7.00%
Dried Blood.	2.00%
Pollard.	5.00%
Wheat.	30.00%
Barley.	30.00%
Salt.	0.25%
Vitamin Premix.	1.00%

TABLE A4.2

Composition of 'BARKO' Dog Sausage:

Minimum Crude Protein.	10.0%
Maximum Crude Fat.	27.0%
Maximum Crude Fibre.	0.7%

TABLE A4.3

Composition of 'Animal Food Pellets'.

Milk Powder.	11.00%
Dextrose.	11.00%
Calcium Phosphate.	25.00%
Farex.	50.00%
Gelitine.	0.70%
Magnesium Stearate.	2.30%

Table 6:1. A Summary of the categories of behaviour.

A: Rats.

Name of Behaviour	Symbol	Other Names	Overall - Category Classif-ication.	Analysis Category No.
Head in food receptacle Eating	H E		*Immediate food - oriented behaviour.*	1.
Ambulation Sniffing Rearing	A S R	Locomotion	*Active investigatory behaviours.*	2.
Drinking	D	Polydipsia/ Licking	*Schedule-induced polydipsia.*	3.
Grooming Stationary	G F	Freezing	*Stationary behaviours.*	4.
Miscellaneous	M	Defecation, urination, pica, gnawing, climbing.	*Miscellaneous.*	4.
B. Ferrets.				
Head in food receptacle Eating	H E		*Immediate food-oriented behaviour.*	1.
Head in food receptacle but immobile Immobile	Hi I		*Stationary behaviours.*	2.
Sniffing	S		*Sniffing.*	3.
Scratching Scrabbling	Sct Scb		*Scratching behaviour.*	4.
Miscellaneous	M	Defecation, licking, rearing, grooming, ambulation.	*Miscellaneous.*	5.